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CONTENTS

No. 1, March, 1932

PAGE

Water Regulation and Its Evolution in the Fishes.....*Homer W. Smith* 1
Ecology of Populations.....*G. F. Gause* 27
Some Developmental Risks. The Dorsal Mid-Line.....*N. William Ingalls* 47
Eutely or Cell Constancy in Its Relation to Body Size.....*Harley J. Van Cleave* 59
Senescence, an Inherent Property of Animal Cells.....*N. R. Dhar* 68
A Critique of Certain Earlier Work on the Inheritance of Duration of Life in Man.....*I-Chin Yuan* 77
Aesthetic Notions in Animal Breeding.....*Walker Van Riper* 84
The Recapitulation Theory.....*Waldo Shumway* 93
New Biological Books:
Brief Notices..... 100

No. 2, June, 1932

The Rôle of Genetics in Etiological Pathology.....*George K. K. Link* 127
The Influence of Temperature on the Life Processes and Death of Bacteria *Bettylee Hampil* 172
The Population of a Nest of the Hornet *Vespa maculata*.....*Barbara J. Betz* 197
The Utilization of Water Colloids and Materials in Solution by Aquatic Animals with Special Reference to Mosquito Larvae.....*E. Harold Hinman* 210
New Biological Books:
Brief Notices..... 218

No. 3, September, 1932

The Hereditary Factor in Human Neoplasms.....*Madge Thurlow Macklin* 255
The Present Status of Problems Relating to the Ciliates of Ruminants and Equidae.....*Elery R. Becker* 282
Modern Research on Human Twins.....*A. B. Droogleever Fortuyn* 298
A Peculiar Roosting Habit of Bats.....*T. Barbour* 307
Sex Differences in Mortality in Abraxas-Type Species *John W. MacArthur and W. H. T. Baillie* 313
The Sensitivity of Fishes to Sound and to Other Mechanical Stimulation *Lucien H. Warner* 326
New Biological Books:
God Means Anything Today.....*Francis P. LeBuffe, S.J.* 340
Brief Notices..... 345

No. 4, December, 1932

Why Aristotle Invented the Word Entelecheia.....*William E. Ritter* 377
Biological Peculiarities of Oceanic Islands.....*Addison Gulick* 405

Temperature Relations of Seed Germination.....*Thomas I. Edwards* 428
Recent Methods of Generating Sound Stimuli for Use in Testing the Auditory Capacity in Animals.....*Meredith P. Crawford and Everett G. Brundage* 444
The Excretory System as a Method of Classification of Digenetic Trematodes
Ernest C. Faust 458

New Biological Books:
Biochemistry and Development.....*George B. Wislocki* 469
Brief Notices..... 474
The Cost of Biological Books in 1932.....*John R. Miner* 498
Index to Volume VII..... 501

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THE QUARTERLY REVIEW
of BIOLOGY

WATER REGULATION AND ITS EVOLUTION IN THE FISHES

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THE regulation of the water content of the body is a physiological problem which has been faced by the vertebrates throughout the course of their evolution. The present paper is a résumé of the essential features of the regulation in the teleost and elasmobranch fishes, and an attempt to interpret the physiological phenomena in terms of evolutionary history. It is convenient, therefore, to preface the physiological discussion with a brief comment on the habitat of the early vertebrates.

Thirty years ago most investigators held the view, expressed implicitly if not explicitly in their writings, that the vertebrates had been evolved in the stable waters of the sea, and that it was as highly organized forms, fitted for swift and powerful motion, that they had penetrated into fresh water rivers and lakes. But there has been since then an increasing tendency to invert this story, and to believe that the early fishes, if not the first vertebrates themselves, were evolved in the continental fresh waters, and that it was only as highly organized forms that they penetrated into salt water.

This shift in view-point has hinged to a large extent upon the interpretation of the origin of the fossil beds in which the early vertebrates are found. The first to advance the fresh-water habitat theory was Chamberlain ('00) who expressed the belief that the vertebrates had been evolved in the continental fresh waters and that here had been the cradle of their evolution throughout Silurian and Devonian time. Chamberlain suggested that the persistent motion of swiftly flowing rivers had played the dominant rôle in impressing upon some lowly aggregate of animal cells, still plastic and indeterminate in organization, the essential features of the vertebrate body: a spindle-like form, a lateral flexibility and a set of longitudinal side muscles adapted to rhythmical contraction. In the transitional stages between the Silurian and the Devonian Periods fish remains appear on both continents, and before the Devonian has passed they present a rich and varied

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deployment embracing not only the two classes *Agnatha* and *Pisces*, but all the known subclasses of these. Yet nowhere, according to Chamberlain's interpretation of the geological record, do fish remains appear abundantly in the open sea deposits. They are confined chiefly to the sediments of inland waters or of littoral zones or of embayed arms of the sea. In the Ludlow bone-bed of England, where fish first make their appearance in abundance, their fossils are associated with the remains of eurypterids, land plants and fresh water molluscs. The total absence, as Chamberlain saw it, of marine relics from the same beds led him to conclude that both the fishes and eurypterids were denizens of fresh water. On the other hand, these same fishes, heavily armoured or toothed as many of them were, are absent from the definitely marine beds in which the imprints of soft medusae and delicate graptolites are preserved. Occasional inclusions of fishes in marine beds might result from carcasses drifting to sea, but the record as a whole convinced him that the fishes were not at this time established as marine dwellers.

It should be recognized, we think, that Chamberlain's interpretation of the fresh-water habitat during Silurian-Devonian times should stand apart from the thesis that the first vertebrates were evolved in this medium, for there was perhaps a long series of intermediate but lowly forms to bridge the gulf in time and space between the first fossil vertebrates, which were relatively highly organized forms, and the ancestral invertebrate stock.

The importance of the eurypterids lies in their constant association with the early fishes; this association has frequently been remarked as one of the most unique faunal and physical combinations of geological history. Clarke and Ruedemann ('12) in summarizing their study of the eurypterids of New York, concluded that these animals lived in the sea from Cambrian to Silurian time, and only later (i.e., in the Devonian and Carboniferous) invaded and ultimately became largely restricted to fresh water. This conclusion tends to invalidate Chamberlain's argument, but set against it are the contrary opinions of Grabau ('13) and O'Connell ('16). O'Connell concluded, after analyzing the faunal associations in a large number of beds, that the eurypterids had lived in fresh water throughout their entire phylogenetic history. While no attempt was made by O'Connell to prove the fluviatile habitat of the fishes, yet the Ludlow bone-beds seemed to her capable of explanation on no other hypothesis. Regarding the constant association of the eurypterids and fishes, she remarked, "This single faunal fact would be sufficient, even though all other types of evidence were wanting, to make me say that those two groups of organisms lived in the rivers." Some authorities (Pirsson and Schuchert, '15; Grabau, '24) have explicitly accepted O'Connell's conclusions with regard to the eurypterids, but neither Ruedemann ('16) nor Clarke ('27) have done so.

In setting forth his somewhat novel hypothesis of the fresh-water origin of the vertebrates Chamberlain did not attempt an exhaustive analysis of the many fossil beds in which fishes are found. Two investigators since Chamberlain have done this, however, and with special reference to the habitat problem: Barrell ('16b) has critically considered certain Silurian-Devonian strata, and MacFarlane ('23) has attempted an interpretation of the whole record up to recent time.

The first vertebrates to appear in the fossil record of Europe are the ostracoderms and early elasmobranchs of the Silurian-Devonian Periods. These periods are well represented and were first extensively studied in the British Isles where the repre-

sentative strata consist largely of red sandstones, shales and conglomerates. Since red sandstone is the predominate outcropping rock, this series has long been known collectively as the Old Red Sandstone. This series was interpreted as lacustrine deposits by Godwin-Austen in 1855, and this interpretation has been reinforced and accepted by many British and American geologists. But the red sandstone has been interpreted by Barrell ('16a) to be a deposit laid down in intermontane basins which were periodically flooded, rather than in stable lakes or estuaries. Intercalated between the freshwater sandstones there are shales and mudstones, carrying a fauna identical in many respects with the underlying and distinctly marine Ludlow. These marine facies represent the temporary recurrence of brackish water, permitting for a time the incursion of a fauna related more to the open sea than to the land. The remaining facies, according to Barrell, were laid down by the rivers of a large Silurian-Devonian continent which was furrowed with mountains and basins. Erosion was rapid, and the climate was marked by seasonal rains separated by periods of great aridity. In the light of his interpretation of the conditions under which these strata were formed, Barrell concluded that the Silurian and Devonian ostracoderms, arthrodires, elasmobranchs and ganoids lived in the fresh waters of the continents, though they were rarely preserved as fossils in the fresh water beds because the conditions under which these beds were laid down were entirely unsuitable for fossilization. The increasing aridity of the Devonian with its periodic droughts served to drive at least some of the sharks and arthrodires into the sea and gave the domination of the continental waters over to the air-breathing ganoids and newly evolved amphibians.

Barrell's interpretation is reinforced by the fresh water nature of many other Silurian-Devonian fish-bearing strata. Kiaer ('24), writing of the ostracoderms of Norway, remarks that the sediments containing these fossils were deposited upon great, extensive flood plains, and that the animals lived in the rivers, lakes and estuaries of the North Atlantic Continent during younger Silurian time. Similarly the Downtonian and Lower Devonian fishes of Spitzbergen are found in sandstones and conglomerates bearing ripple marks and are associated with land plants as well as lamellibranchs, ostracods and molluscs (Stensiö, '27). A continental origin has been ascribed to the lower Devonian fish-bearing strata of Russia (Geikie, '23), Greenland (Woodward, '00) and many North American beds (Grabau, '21).

MacFarlane ('23) has considered in detail the faunal relationships and the geological character of the fish-bearing strata from the earliest to recent times. He has drawn the conclusion that not only the fishes, which he believes to have been evolved from a metanemertean ancestor, but all organic life, evolved in fresh water and that from this environment successive organismal invasions of the sea first, and of the land at a later period, started the main groups of marine plants and animals as well as land types.

Again we believe it proper, at least for the present discussion, to recognize that the argument may be separated; the evidence on the habitat of the Palaeozoic and Mesozoic fishes should be considered independently of any theory of the origin of organic life in general, or even of the vertebrates themselves.

MacFarlane concludes that the primitive vertebrates and the eurypterids of the Silurian Period, and the Devonian ostracoderms, elasmobranchs, dipnoans and

ganoids were inhabitants of the continental fresh waters the world over. None are met with, he states, alongside marine organisms in definitely marine beds of the periods. During the late Devonian or early Carboniferous a seaward migration of some elasmobranchs began, these forms giving rise to the marine elasmobranchs of the Carboniferous Limestone or Upper Mississippian Period. These marine forms were obliterated by the close of the Carboniferous Period, however, and it was not until the Jurassic and Cretaceous that a new migration of elasmobranchs seaward was effected by forms that had been evolved in the meantime in the continental waters. Of these, only a few genera (Rhina, Rhinobatus, Notidanus, Cestracion, Pristiurus, etc.) have survived to the present. The majority of marine elasmobranchs of today represent forms which, evolved in fresh water, have migrated into the sea since the opening of the Eocene.

Although a few ganoid forms may have become established in a marine habitat in the Carboniferous, Permian and Triassic, it was not until the Jurassic and more especially the Cretaceous that any considerable seaward migration occurred; but these in turn were practically obliterated, like the Cretaceous elasmobranchs, and the recent marine teleosts represent derivatives of stocks that for the most part have been marine only since the Eocene.

The evidence seems to be interpreted alike by the above authors that Cambrian and Silurian ostracoderms were fresh water inhabitants, at least primitively. There is no fossil record of the recent cyclostomes (which, according to Stensiö ('27) are primitive but slightly modified ostracoderms), but it is significant that some of them are still anadromous, returning to the continental waters to spawn.

Thus, if we accept MacFarlane's view, we must believe that the recent crossopterygians, the ganoids and some of the teleosts (such as the Ostariophysi, nearly all of which are fresh water forms or return to fresh water to spawn) have had a continuous fresh water ancestry since the first definitive fishes were evolved. A few elasmobranchs have been marine dwellers, perhaps, since the Cretaceous, but most of them only since the Eocene. The greatly diversified and numerous marine teleosts of today have been inhabitants of the sea for no greater period of time, some families (Albulidae, Chirocentridae, Clupeidae, etc.) having had an anadromous or marine habit at the most only since the Cretaceous. MacFarlane points out that certain morphological changes are associated with a strictly marine habitat: the disappearance of the air bladder (which comes down to the primitive and fresh water fishes as an inheritance from their Devonian air-breathing ancestors); an increase in the number and distribution of the dorsal fin spines and the movement of the pelvic fins into the thoracic or even jugular position. It is perhaps significant that many strictly marine forms have undergone marked specialization, like the Fistularidae, Syngnathidae, Blennidae, Pediculati and the deep sea fishes generally, but there is no universal morphological tendency which is invariably associated with a marine habitat. Unquestionably many derivatives of long established marine stocks have secondarily reinvaded fresh water, as for example some elasmobranchs (Engelhardt, '13), the common eel, the pipe fish, the toad fish, etc. There may have been many migrations between salt and fresh water, and the interpretation of the history of any one genus or family remains a very complex affair.

MacFarlane's interpretation is admittedly the most extreme view of the fresh water habitat problem. It suffers, perhaps, in being associated with a specific

theory of the fresh water origin of the vertebrates, as is the case with Chamberlain's theory, but when dissociated from this admittedly speculative feature, we know of no evidence that positively contradicts it. Chamberlain, Barrell and MacFarlane are essentially in agreement up to the close of the Devonian, and MacFarlane is the only one who has attempted an analysis of the record beyond that date.

We are aware from conversations with palaeontologists and geologists that the fresh water theory has been received with scepticism, but no specific criticisms of Chamberlain or Barrell's interpretation of the Devonian record, as such, has been brought to our notice. The theory of the fresh water origin of the vertebrates as postulated by Chamberlain has been criticized by Berry ('25) on the grounds that the form and metamerism of the fishes should be explained as the result of the dynamics of a moving organism within a static medium, rather than conversely. Gregory ('28) has pointed out that the earliest known fishes were short-bodied and very unlike an eel, and it seems probable that the first chordates were by no means eel-like free-swimming forms but somewhat depressed and partly bottom-living forerunners of the anaspid ostracoderms. This criticism does not bear upon the actual habitat of the Palaeozoic forms, however. Chamberlain's dynamic theory is not widely accepted, but the fresh water habitat ascribed to the Silurian and Devonian fishes by both Chamberlain and Barrell has been tacitly accepted by Grabau ('21), Pirsson and Schuchert ('15), Geikie ('23), Lull ('29) and others. Zittle ('23) accedes that the oldest fishes may have been fresh water inhabitants, but like many other commentators, he considers the later Palaeozoic and Mesozoic forms to have radiated from a marine habitat. In addition, there are of course a great many papers dealing with particular beds, but the short space of this review limits it to the few authors who have commented specifically upon the habitat problem.

II

Beginning with the observations of Bert ('71), Mosso ('90) and especially of Bottazzi ('97) on the fishes, and of Bunge ('98) and Quinton ('97) on the blood of higher animals, a large number of papers have appeared dealing with the osmotic pressure and salt content of the blood of various animals under normal and artificial conditions. The literature on these subjects is well summarized by Bottazzi ('08), Scott ('16), Schlieper ('30) and by Schulz and Krüger ('25) and it is only necessary to restate some outstanding features here.

The body fluids of most marine invertebrates have the same osmotic pressure as that of the external medium. A few are observed to be hypertonic to sea water (Schlieper, '30) showing that in some instances a degree of osmotic control in media of high osmotic pressure has been achieved. The fresh water and euryhaline invertebrates maintain an osmotic pressure in their body-fluids significantly above that of the external medium, but nevertheless considerably below that which characterizes marine forms.

In contrast to the invertebrates, the teleosts are characterized by a nearly steady osmotic state; the blood of salt water fishes generally has only a slightly higher osmotic pressure than the blood of fresh water fishes, and a very slight change is observed in euryhaline forms when transferred from one medium to another. Most teleosts which live exclusively in fresh or salt water die if they are removed from the one medium to the other. In the case of the fresh water carp, for example, the osmotic pressure of the blood rises markedly before death in

salt water (Duval, '25) but this result may be due to a quantitative inability to effect the necessary readjustments and continuous regulation with sufficient rapidity, rather than to a qualitative difference in physiological organization as compared with the euryhaline forms. The available evidence indicates that the teleosts as a whole constitute a uniform group in regard to the physiological regulation of the composition of the blood, though in some species the physiological capacities are less effective than in others. If so, we can say that the fishes are divisible into two physiological groups, the elasmobranchs and the teleosts, which differ qualitatively in the nature of the regulation which they impose upon the blood, and in the *modus operandi* of this regulation. The teleosts as one group tend to maintain a constant osmotic pressure in their body fluids whether they live in fresh or salt water, while the elasmobranchs allow the osmotic pressure of their body fluids to rise as the salinity of the external medium is increased, so that in marine forms the blood is still hypertonic to the sea water in which they live.

In order to analyse the regulatory processes which are at work in both these groups, it will be convenient to state briefly the osmotic problem faced by a hypothetical organism moving from fresh to salt water:

In fresh water the organism, by virtue of the salt content of its tissues and body fluids, is osmotically superior to its environment (i. e., it has the higher osmotic pressure) and in consequence of this fact water tends to pass from the external medium into the body and at the same time salts tend to diffuse from the body outward. For most purposes it makes little difference whether we consider the movement of water (and salt) as occurring through the skin and gills, or as a consequence of the ingestion and absorption of water from the gastrointestinal tract; the net result of the natural osmotic exchange is the same—the body tends to become "diluted" in its internal composition. In order to maintain a constant composition, such a fresh water organism must be able to compensate for this dilution by excreting from its body a solution (urine or otherwise) which is more dilute than its blood. We will find it convenient to refer to this physiological operation as *hypotonic excretion.*

In salt water the situation is reversed; the (homoiosmotic) organism is osmotically inferior to its environment, and in consequence of this reversed osmotic gradient, water tends to move out of the body and salts tend to enter. Thus the organism tends always to become more "concentrated," and in order to compensate for the inevitable exchanges of water and salt it must excrete from its body a solution which is more concentrated than its blood. This process we will designate as *hypertonic excretion.*

There is little physicochemical difference between hypotonic and hypertonic excretion, for both processes require that the organism separate from its blood a fluid of dissimilar osmotic pressure, and both require the expenditure of energy in the performance of physicochemical work. To switch from one process to another one might suppose, to put it roughly, that all that would be required would be to turn an excretory mechanism around so that it would have reversed orientation with respect to the blood. But physiologically the problem is not so simple, for the orientation of the "excretory mechanisms" in the vertebrates was apparently fixed early in their evolutionary history, and consequently we find a wide separation of hypotonic and hypertonic excretion as physiological processes. It is this fact which

appears to lie at the heart of the whole problem of osmotic regulation. This physiological limitation is clearly demonstrated when we consider the rôle which the kidneys play in this regulation, for it appears that these organs are capable of excreting a urine which is hypotonic to the blood in all vertebrates; while the capacity to excrete a hypertonic urine is not acquired by the kidneys until the birds, or possibly the mammals, are reached.

This distinction is brought out in Table I, which contains data on the urine collected from animals living in fresh or salt water, or after desiccation or the administration of salt. It is under the last three conditions, of course, that we would expect the urine to reach its greatest

TABLE I

Maximal and minimal osmotic pressure of the urine in relation to the blood

	Δ °C., MEDIUM	Δ °C., BLOOD	Δ °C., URINE	OBSERVER
ELASMOBRANCHII				
Pristis macrodon	0.03	1.02	0.10	Smith, '31a
Scylliorhinus acanthias	2.15	2.36	2.23	Bottazzi, '06
Torpedo marmorata	2.15	2.20	2.24	Bottazzi, '06
Scylliorhinus caniculus	2.15	2.33	2.21	Buijtendijk, '09
Squalus acanthias	1.85	1.95	1.87	Smith, '31b
Raja stabuliforis				
DIPNOI				
Protopterus aethiopicus	0.03	0.48	0.09	Smith, '30b
TELEOSTEI				
Amia calva	0.03	0.54	0.07	Original
Lepidosteus osteus	0.03	0.57	0.08	Original
Anguilla rostrata	0.08	0.63	0.09	Original
Anguilla rostrata	1.85	0.82	0.79	Original
Orthagoriscus mola	2.15	0.80	0.69	Rodier, '99
Anarrhichas lupus	1.73	0.68	0.63	Dekhuysen, '05
Gadus virens	1.73	0.76	0.63	Dekhuysen, '05
Gadus morrhua	1.73	0.73	0.65	Dekhuysen, '05
Lophius piscatorius	2.15	0.86	0.80	Bottazzi, '06
Conger vulgaris	2.15	1.03	0.82	Burian, '10
Scorpaena scrofa	2.15	0.71	0.65	Burian, '10
Myoxocephalus octodecim	1.85	0.82	0.78	Smith, '30a
AMPHIBIA				
Rana esculenta	0.01	0.44	0.17	Bottazzi, '08
Rana sp.	0.70	0.74	0.70	Brunacci, '14
Rana sp.	0.77	0.75	0.85	Brunacci, '14
REPTILIA				
Emys europa	Terrestrial	0.44	0.10	Bottazzi, '08
Testudo graeca	Terrestrial	0.60	0.19	Burian, '10
Thalassochelys caretta	Marine	0.65	0.61	Burian, '10
Caretta kempi	1.85	0.66	0.64	Original
Caretta caretta	1.85	0.76	0.70	Original
AVES				
Chicken	Normal	0.62	0.79	d'Errico, '07
Chicken	Hypertonic salt	1.09	0.89	d'Errico, '07

osmotic concentration. These observations show that the urine of fresh water elasmobranchs, teleosts and Amphibia, and of the mammals during water diuresis, is typically very dilute, and it is quite probable that equally dilute urine could be obtained from the reptiles and birds under conditions which would produce a marked water diuresis.

On the other hand the urine of elasmobranchs and teleosts living in sea water approaches the blood in osmotic pressure, but never exceeds it. Brunacci ('17) and Przylecki ('22) found that the urine of the frog never became osmotically more concentrated than the blood, even when the animal was immersed in or injected with hypertonic salt solutions. (Incidentally it may be noted that the blood of the Amphibia remains hypertonic to the medium in which they are immersed, up to the lethal concentration. Cf. Adolph, '27 and Duval, '28.) Burian ('10) found that the urine of the tortoise, *Emys europa*, under conditions of water deprivation, and the normal urine of the marine turtle *Thallassochelys caretta*, were hypotonic to the blood; similar unpublished observations have been made by us on the marine turtles *Caretta kempi* and *Caretta caretta*. These facts leave it quite certain that the fishes, the Amphibia and the reptiles are incapable of excreting a hypertonic urine. According to d'Errico ('07) the ureteral urine of the chicken when collected by cloacal catheter is normally slightly hypertonic, but it acquires a hypotonic relation after the intravenous injection of strong salt solutions. In sharp contrast to all the above, it is well known that the urine of mammals can have an osmotic pressure several times that of the blood. It is in the mammals only, apparently, that hypertonic urinary excretion is well developed. Crane ('27) has pointed out that since the chief anatomical difference between the kidneys of the lower animals and the mammals lies in the presence in the latter of the loop of Henle, it may be here that the reabsorption of water against osmotic pressure occurs. Huber ('17) states that a well developed loop is present in a small fraction of the tubules of the chicken kidney, which fact may account for the slight hypertonicity of the urine observed by d'Errico. However, since this investigator permitted the urine to enter the cloaca, where water absorption is known to occur, the slight hypertonicity noted by him is of doubtful significance.

We may take it, then, that in the evolution of the vertebrates a hypertonic excreting kidney was not evolved until the mammals. As remarked above, this fact is an important one in the problem of the regulation of the body fluids, for the marine fish is required to separate water for the formation of its physiologically hypotonic urine from the concentrated sea water in which it lives. Since the separation of water from a salt solution (or from sea water) requires the expenditure of energy in the form of osmotic work (in concentrating the residual salt solution, so to speak) this procuring of water for urine formation becomes a physiological problem of the first order. The significance of this fact was well recognized by Dekhuyzen ('04) who remarked, " . . . Es muss ein Organ geben welches bei den Teleostien Wasser aus dem Seewasser, dem osmotische Druck entgegen, resorbirt oder ein anderes Organ als die Niere, welches Salze ausscheidet."

Of Dekhuyzen's alternative explanations, the last appears to be the correct one, for as recent experiments have shown, the marine teleost persistently "drinks" sea water in larger or smaller amounts, absorbs most of the water and salt into its blood, excretes the salts *extrarenally* and leaves the water free for the formation of

hypotonic urine, in compliance with the osmotic limitations of its kidneys (Smith, '30a). There are a number of reasons for thinking that the extrarenal excretion of the salt is effected by the gills, but in any case it is in this process that the osmotic work is done which enables the fish to manufacture continuously a dilute urine from the concentrated sea water which surrounds it. It is impractical to review the experimental methods, etc., here, but the more important lines of evidence will be described. For details, the reader is referred to recent papers mentioned in the text.

TABLE II

Composition of gastrointestinal fluids and urine of marine teleosts (Smith, '30a)

	Δ °C.	MILLIMOLS PER LITER							
		Na	K	Ca	Mg	Cl	SO_4	PO_4	CO_2
Sea water (Sandy Hook)	1.33		4.6	8.0	33	350	26	0.0	2.0
Lophius piscatorius									
gastric fluid	1.06	122	117.0	8.2	5	174	6	6.2	23.2
ant. intest. fluid	1.04	143	77.0	15.2	60	90	94	9.6	34.2
post. intest. fluid	0.83	128	37.0	18.8	92	72	122	5.0	60.5
urine	0.64		7.6	14.8	75	161	36	14.7	1.2
Sea water (laboratory)	1.81		8.3	10.3	44	457	31	0.0	3.0
Anguilla rostrata									
intest. fluid	0.75		0.6	11.3	139	76	122		
urine	0.66		5.7	7.5	75	76	52		
Sea water (Frenchman's Bay)	1.85		9.2	10.0	49	505	30	0.0	2.4
Myoxocephalus octodec.									
intest. fluid	0.75		0.1	101.5	67	122	109	0.0	42.6
urine	0.78		0.1	23.6	114	129	54	16.0	

The significant features of the salt and water cycle in the marine teleost are illustrated by the data given in Table II.

It will be noted from the composition of the gastrointestinal fluids that as the ingested sea water passes from the stomach through the intestine, the Mg and SO_4, which are poorly absorbed, become concentrated several times by the absorption of water and some of the other salts which are contained in the sea water (Na, K, Cl and Ca). At the same time the osmotic pressure of the gastrointestinal contents decreases; in the stomach a mixture of sea water with gastric juices gives a fluid somewhat hypertonic to the blood but, as water and salt are absorbed from the intestine, the osmotic pressure of the residue falls and approaches that of the blood. This fact shows that the gastrointestinal tract itself is essentially an indifferent "absorber," in that it does not absorb water against osmotic pressure, and that it does not play any part in separating salt from the water that is destined to be excreted as urine. This result is consonant with what is observed in mammals, where fluids introduced into the gastrointestinal tract invariably approach osmotic equilibrium with the blood (Goldschmidt, '21). Apparently the vertebrate gastro-intestinal tract has never acquired the capacity to absorb water against osmotic pressure.

Having swallowed and absorbed sea water and most of its contained salts, the marine fish has become "concentrated,"

because, with respect to its own body fluids and tissues, it has absorbed relatively more salt than water. It is essentially in the same position as though it had lost some of its body water to the surrounding sea. Since the urine which is formed from this absorbed water and salt is much more dilute than the ingested sea water, it follows that within the organism salt is separated from water and excreted extrarenally, while the water is left free to be excreted as urine. As an independent and confirmatory line of evidence leading to this same conclusion, we may turn to the excretion of the several salts. The salts in the urine of marine fish consist principally of Mg, Ca, SO_4 and PO_4, there being very little Na, K or Cl present under normal conditions. Even in a carnivorous fish like *Lophius*, after a large meal of meat, K appears in the urine only in traces and Cl in small amounts. The presence of Mg and SO_4 in the urine is attributable to their absorption from the highly concentrated sea water residue in the intestine, but in spite of the fact that probably only small amounts of these substances gain access to the body in comparison with the large amounts of Na and Cl absorbed, they usually predominate over the Na and Cl in the urine. This fact is additional evidence that the univalent salts are excreted from the body by some route other than the kidneys.

Lastly, the fate of water itself can be roughly followed by the use of a dye such as phenol red. The urine can be collected while the fish is immersed in the dye solution, and the ingested dye can be recovered from the intestine and quantitatively determined. In this way it can be shown that only a fraction of the water which is absorbed in any given period of time is excreted as urine. Since the fish does not gain in weight, it follows that part of the absorbed water itself must be excreted extrarenally.

So the evidence shows that the marine teleost is simultaneously performing three operations:

a) Excreting water extrarenally. (As shown by phenol red experiments.)

b) Excreting univalent salts extrarenally. (As shown by the predominance of Mg and SO_4 over Cl in the urine.)

c) Doing osmotic work extrarenally and extraintestinally. (As shown by the elaboration from ingested sea water of a dilute urine and intestinal residue.)

It is reasonable to suppose that these three operations are identified with a single process, in which case the fish *must be excreting extrarenally a salt solution which is not only hypertonic to its blood, but also to the ingested sea water*, and thus freeing water for the elaboration of its dilute urine and intestinal residue. Thus, osmotic regulation in marine teleosts is effected by extrarenal organs which are capable of hypertonic excretion, since the kidneys and intestinal tract are not capable of this operation.

The extrarenal excretion of salt is not directly demonstrable in sea water, but it can be demonstrated easily in fresh water teleosts to which various salts have been administered by rectum. By collecting the urine with a retention catheter it can be shown that most of the administered Na, K and Cl are excreted extrarenally while Mg, Ca, SO_4 and PO_4 are excreted only by the kidneys. (Professor E. K. Marshall advises me that iodide is also excreted predominantly by the extrarenal route in the marine toad fish.) By placing a fish in a "divided box" separated into an anterior and posterior chamber by a partition of rubber dam fitting tightly around the fish's body, it can be shown that the extrarenal excretion of Na, K and Cl is

confined to the anterior part of the body. It seems probable, though there is no proof, that this process is carried out by the gills. Our principal reason for thinking this, is that the extrarenal excretion of salt by marine fish is a process involving the performance of osmotic work, and one that is of the greatest physiological importance to the organism in the regulation of the composition of its body fluids, not only with respect to salts, but also with respect to water. We would expect, therefore, that it would be associated with a blood supply nearly as abundant as respiration itself.

Since this paper was submitted for publication Keys ('31) has reported the direct demonstration of the secretion of chloride and water by the perfused head (gills?) of *Anguilla vulgaris* in sea water, thus confirming the conclusions reached above. Keys calculates that the gills are capable of doing as much osmotic work per gram of tissue as the mammalian kidney. His interesting paper unfortunately appeared too late to be discussed in detail here.

The fresh water teleost apparently does not drink water but absorbs it through the oral membranes or perhaps through the gills. Nevertheless, the urine flow in them is very large, ranging from 100 to 150 cc. per kilogram per day. In contrast to this abundant urine formation, the marine fish excretes a very small quantity of urine. This reduction in urine flow results partly from the fact that a large fraction of the ingested and absorbed sea water is excreted extrarenally, and partly from the fact that nearly all the water excreted as urine must be procured from sea water at the expense of considerable osmotic work in the extrarenal disposal of the contained salts. Consequently the normal fish tends to keep the urine flow and the ingestion of sea water down to a minimum for the sake of physiological economy.

Because of the ease with which marine fish are injured, it is difficult to obtain them or to keep them in captivity in a normal condition. Grafflin ('31) has found that small trifles such as handling a fish, rough live-cars, etc., result in the production of a marked diuresis. He attributes this result to almost insensible injuries to the skin. The urine flow may be increased many fold, and with the increased excretion of water, the total urinary nitrogen becomes correspondingly dilute. The normal urine of the fish which Grafflin examined (toadfish and sculpin) is essentially Cl free, but as the diuresis develops the blood Cl rises and Cl appears in the urine in increasing amounts.

Portier and Duval ('22) have shown that the power of osmotic regulation of the eel is greatly impaired by traumatizing the skin and removing the slime by vigorous wiping. They interpreted their results as showing that the skin plays an important part in the regulation of water exchange, but we have pointed out that their results are open to another interpretation, namely, that trauma of the skin and removal of the slime impairs the normal integumentary insulation and permits sea water to draw water out of the body osmotically. Under these conditions the physiological machinery normally operating to maintain the composition of the blood would be overtaxed. It seems to us that the same explanation applies to the diuresis observed by Grafflin; where the skin is injured, water is drawn out of the body and the blood tends to become more concentrated; as this process continues it leads to an increased ingestion of sea water, an increased extrarenal excretion of salt and an increased urine flow induced by the Mg and SO_4 absorbed from the intestinal tract, for these substances are only excreted by the kidneys. (Bieter ('31) has recently shown that Mg and SO_4 exert a

marked diuretic effect in aglomerular fish, and there is little doubt that they have a similar effect in glomerular fish.) That the diuresis is a result of an increased excretion of Mg and SO_4 is indicated by Grafflin's observation that as the diuresis develops the total quantity of SO_4 which is excreted also increases (he did not follow the Mg excretion); but this fact does not, of course, exclude other factors such as increased blood Cl, from contributing to the same end.

It is interesting to note, in passing, that the alkaline nature of the intestinal secretions favors the formation and precipitation of MgO, and thus liberates from the concentrated intestinal residue, rich in Mg, a further moiety of water for isotonic intestinal absorption. We have observed that *Anguilla*, while living undisturbed in quite concentrated sea water ($\Delta = 2.5°C$) deposits solid pellets of MgO mixed with carbonates and sulphates on the floor of the aquarium, showing that the ingestion of sea water is a practically continuous affair in undisturbed fish.

III

The elasmobranch fishes are distinguished from all other vertebrates by the presence of large amounts of urea in the blood, the tissues and all the body fluids. Since the discovery of this interesting fact by Staedeler and Frerichs ('58) numerous analyses of the blood or tissues of various species have been made. This "uremia" is present in all species of the Selachii, Batoidei and Holocephali which have been examined; the urea permeates the blood and all the body fluids, the tissues, the gastro-intestinal tract and the bile, and may amount to as much as 3 grams per 100 grams of water.

The presence of such large quantities of urea in the elasmobranchs has been diversely explained as due to a specific affinity of the tissues for this substance (Krukenberg '88), a special function with regard to the heart and other organs (Baglioni '05) and the inability of the kidneys to excrete it (von Schroeder '90; MaCallum, '26). We do not think that any of these explanations are correct, but believe that the urea plays a direct part in maintaining the water equilibrium of the body.

Through the favor of the John Simon Guggenheim Memorial Foundation we have recently had the opportunity to extend our knowledge of the osmotic relations of these fishes by an examination of fresh water forms (Smith, '31a). Our results, when coupled with data on marine forms (cf. Smith '29a, '31b), make it possible to trace the water and salt cycle, as in the teleosts.

The elasmobranch possesses, at least in a rudimentary way, the fundamental character of the teleost; for like the latter it absorbs water, Na, K, Ca, Cl and some Mg and SO_4 from the gastrointestinal tract, and excretes most of the Na and Cl extrarenally and the Mg and SO_4 in the urine. But superimposed (we use the word guardedly) upon this teleost mode of regulation there is in the elasmobranchs a special urea mechanism. They have evolved branchial and oral membranes that are relatively impermeable to urea, as is shown by the fact that high concentrations of this substance are normally retained by them within the body. In addition, they practice the renal conservation of urea by reducing the urinary excretion to a low level. This conservation is effected, apparently, by reabsorbing the urea from the glomerular filtrate as the latter passes through the renal tubules; the elasmobranch kidney readily excretes glucose and ferrocyanide—substances which Marshall ('30) has shown are not excreted by aglomerular fish—and it is hardly prob-

able that the glomerular membrane would be permeable to these and impermeable to urea. Because of this conservative process, the normal urine of elasmobranchs invariably contains urea at a much lower concentration than does the blood.

Between the retentive action of impermeable membranes on the one hand, and active renal conservation on the other, a physiological "uremia" results so that the urea reaches concentrations that exceed those observed in any other animal except the estivating lungfish, in which renal activity is suspended (Smith '30b). This urea permeates the entire body and, as Fredericq ('03, '22) has pointed out, is probably osmotically and physiologically inert with respect to the tissues, but because the gills and integument of the animal are relatively impermeable to it, it exerts a significant osmotic pressure with respect to the external environment. In fact, it suffices to raise the osmotic pressure of the blood above that of the external environment, a relationship to which Duval ('25) first called attention. The marine elasmobranch is therefore osmotically superior to the sea water around it, just as is the fresh water fish with respect to fresh water, and this fact permits it to absorb water directly just as does the latter. For this reason the elasmobranch does not need to drink sea water, as does the marine teleost; it can obtain its water for hypotonic urine formation by direct absorption in sea water as well as in fresh water.

The significant features of the osmotic relations of some elasmobranchs are given in Table III, which shows the changes in the osmotic pressure of the blood and urine, and the urea and chloride content of the serum in relation to habitat.

TABLE III

Composition of elasmobranch serum in relation to habitat (Smith, '31a)

	Δ °C., WATER	SERUM			Δ °C., URINE
		Δ °C.	Cl, mM. per L.	Urea N, mg. per cent	
Raja diaphenes	1.850	1.924	272	1000	1.900
Raja stabuliforis	1.850	1.933	257	1091	1.840
Raja sp.	1.484	1.617	224	865	1.065
Raja sp.	1.484	1.607	214	850	0.895
Squalus acanthias	1.330	1.622	234	695	
Raja sp.	1.091	1.227	183	708	0.788
Raja sp.	1.091	1.366	162	583	0.536
Pristis macrodon	0.0	1.02	170	364	0.10
Pristis macrodon	0.0	0.93	169	261	0.10
Dasyatis uarnak	0.0	1.02	212	292	
Carcharhinus melanopterus	0.0	0.90	158	288	
Hypolophus sephen	0.0		146	228	

It will be particularly noted, in passing from the fresh water to the marine forms, that the urea increases about 300 per cent, the osmotic pressure about 100 per cent and the chloride about 60 per cent. The first figure is probably not the maximal for we have observed values for the urea N as high as 1300 mg. per cent (Smith '29a). Clearly, the urea is a substance of physiological indifference to these organisms, except as it serves an osmotic rôle and

facilitates the absorption of water when the animal is in sea water.

If the osmotic pressure of the blood is plotted against the osmotic pressure of the external medium a curve is generated which begins with the blood of fresh water animals at an intersect or "threshold" of $\Delta = 1.0°C.$ and approaches the bisectrix asymptotically. The osmotic pressure of the blood remains always above that of the external medium, but the difference becomes progressively less as the external medium becomes more concentrated.

A similar situation exists in *Myxine glutinosa*. We have observed that the blood removed from animals living in sea water ($\Delta = 1.88°C.$) is hypertonic ($\Delta = 1.98, 1.93, 1.85$) but there is no large quantity of urea present (7 to 13 mg. urea N per cent) and the osmotic pressure is furnished largely by salts (serum Cl 465 to 476 mM. per liter). Dekhuyzen ('04) observed a Δ ranging from 1.736 to 1.829 in the same species. Greene ('04) observed a Δ of 1.966 in the blood of *Polistotrema* (*Bdellostoma*) *stouti* living in sea water the Δ of which was 1.924°C.

It is especially interesting that this apparent hypertonicity does not prevail in *Petromyzon fluviatilis*, for Dekhuyzen ('04) observed that the blood of animals captured at Leiden showed a Δ of 0.473–0.500°C., and Burian ('10) gives 0.586°C. as the Δ of the blood removed from animals which we are led to infer were removed from sea water with a $\Delta = 2.3°C.$ If this difference between *Petromyzon* on the one hand and *Myxine* and *Polistotrema* on the other is real, it indicates profound differences in the physiological character of these groups. It is interesting to note in this connection that Stensiö ('27) says, "..... the Petromyzontia must have evolved either from the Anaspida or from the common ancestors of these and the Osteostraci, whereas the Myxinoidea are descendants either from Palaeospondylus or from the primitive Heterostraci....." It is thus possible that these two groups lead back to a "parting of the ways" in the evolution of body fluid regulation.

Between fresh water elasmobranchs and those living in the Mediterranean, the osmotic pressure of the blood increases from $\Delta = 1.0°C$ to $\Delta = 2.3°C.$ This wide variation in osmotic pressure serves the purpose of supplying water by keeping the organism osmotically superior to its environment at all times. In view of this wide variation it would seem that the osmotic pressure of the blood has no physiological significance itself, except as it serves a rôle in the absorption of water; like the blood urea, the total osmotic pressure is but a means to the end of water regulation, and without independent significance. We are led by this conclusion to question the physiological importance of osmotic pressure in other animals.

Opposed to this interpretation there is the approximate constancy of the osmotic pressure of the blood of fresh water and marine teleosts (Dakin, '08a), and of the higher animals. But in answer to this objection we would point to the fact that, even in the elasmobranch, the salt content of the blood tends to be regulated to narrower limits than either the urea or the total osmotic pressure. It is possible that this salt content—either as total salt or specifically as NaCl together with small quantities of other salts—represents another steady state which tends to be regulated independently to rather narrow limits; and in consequence of a constant water content and a simultaneously constant salt content (which is approximately reached in the elasmobranch and more perfectly in the teleost) there results secondarily, and incidentally, a constant osmotic pressure. The latter would then appear to be a steady state, but its steadiness would be of only secondary physiological importance. It is possible that the salt content of the body is itself of secondary importance; for it may be that when we have a better understanding of the renal and extrarenal mechanisms whereby the water and protein content of the body are regulated, the salt will turn out to be subordinate to these, even as osmotic pressure and urea are subordinate to water absorption in the elasmobranch.

In any case, we are inclined to reject osmotic pressure, *per se*, from the category of Bernard's steady states, and to focus our attention primarily upon the water content of the body.

Several investigators have examined the effects of transferring marine elasmobranchs to diluted sea water or to fresh water (Fredericq, '03; Garrey, '05; Scott '13; Portier and Duval, '22; Chaisson, '30; Margaria, '31). The inevitable result is that the animal absorbs water, gains in weight and ultimately dies. We interpret this result as due to the inability of the kidneys and other tissues to effect the necessary readjustments with sufficient rapidity. Large quantities of urea must be excreted before the body can restore its water intake and output, and therefore its water content, to a normal level. Were the gain in weight observed by these investigators in diluted sea water a part of the final readjustment of the organism, then it would seem that the resulting dilution of the body in strictly fresh water should exclude these fishes from this habitat. Yet some 22 species of elasmobranchs are known to migrate into fresh water and some of them actually live and breed there; these include *Carcharias*, *Sphyrna*, *Pristis*, *Rhinobatus*, *Raja*, *Taenuria*, *Trygon* and *Ellipesurus* (Engelhardt, '13) and there are probably many others.

It is incontestable that the teleosts, as a whole, can and do regulate the water content of their bodies within narrow limits whether they live in fresh or salt water, although individual species die and undergo marked changes in water content if transferred abruptly from fresh to salt water, or *vice versa*. It seems to us that the results of forcing individual elasmobranchs into concentrated or diluted sea water are of no more significance for interpreting the fundamental relations than they would be in the case of the teleosts.

In support of our interpretation, it is significant that the water content of the tissues of all vertebrates is approximately constant and close to 80 per cent, as Gray ('28) has pointed out. It is equally significant, however, that the protein content of the tissues (muscle) has remained essentially fixed throughout the evolution of the vertebrates, varying from 13 per cent in the elasmobranchs to 20 per cent in the mammals (Buglia and Constantino, '12). This narrow range of protein-water composition stands in marked contrast to the widely varying stresses which must operate to alter it in a marine as contrasted to a fresh water habitat, or in terrestrial as contrasted to aquatic life. The extreme instance of protein variation with which we are familiar is in the salmon during the spawning migration, at which time the fish goes without food for 4 to 5 months, swims great distances against swift currents and uses the muscle proteins in the development of the ovaries; at the most, however, the protein content of the fat free muscle changes only from 20 per cent to 14 per cent (Greene, '26). In contrast to this extreme case, it is well known that the protein-water ratio in the tissues of any one species is remarkably constant, and that in the composition of the body, water is the primary and central feature, as has been emphasized by Rowntree ('22) and by Adolph ('30). All these facts suggest to us that the really fundamental steady state in the composition of the vertebrate, whether viewed individually or in the terms of evolution, is the water content of the body; and we suggest, with less certainty perhaps, that this water content is maintained with reference to the tissue proteins.

In closing the discussion of the elasmobranchs, reference may be made to a recent observation of Needham and Needham ('30) that the elasmobranch egg and em-

bryo contain considerable quantities of urea. These investigators suggest that this fact is correlated with the cleidoic or closed-up egg case, for as they say:

"It is evident that survival value attaches to the closed-box egg, for the longer an embryo can continue its prenatal existence the stronger it will be when it at length emerges, and for this end, much more protection is required than for the minute egg whose development is quickly accomplished. It is therefore very interesting that the only class of animals lower than the reptiles which have evolved a structure approaching the cleidoic egg, are just those which have found out a way to withstand a concentration of urea in their bodies which would ordinarily be rapidly fatal. If the *Scyllium* had had to arrange for an efficient removal of its nitrogenous waste-products, it could perhaps not have elaborated its egg-case. But the evolution of the egg-case must have taken place in two stages; first the elasmobranchs, having discovered how to withstand severe uremia, were able to enclose their embryos completely, and secondly when it later became convenient to open the box again, whether for the respiratory water current or other purposes, the selachians, having become adapted to urea-retention, continued to store it within themselves."

We would interpret the facts in the reverse fashion, since we conclude that the adult uses the urea to enable it to absorb water from sea water. According to our interpretation the urea is valuable to the adult but not to the embryo, especially since the latter is inclosed within an impermeable shell, and therefore we view the cleidoic egg of the elasmobranch as an adaptation enabling the embryo to retain its maternal and its own urea in preparation for its adult marine life. It would be interesting to learn when, and in relation to what habitat, the cleidoic egg first appears in the palaeontological record. The issue which we have raised may appear to be only reopening the old query, "Which came first, the chicken or the egg?" But in matters of evolutionary adaptation it seems that we would have to allot temporal priority to the adult. In any case, our interpretation explains why the oviparous elasmobranchs, alone among all fishes, evolved the cleidoic egg, which the alternative view does not explain.

The same issue might be justly raised about uric acid metabolism of the birds and reptiles in relation to arid life, (Needham, '26) for the excretion of nitrogen in a form that conserves water is, in the adult, a matter of just as great importance as is the conservation of water by the cleidoic egg in the embryo.

Lack of space prevents our including here a résumé of the observations that have been made upon the maintenance of water equilibria in Amphibia. The recent papers of Adolph ('31a, b) contain many interesting observations on the mechanism of water absorption in the frog, and show that the skin of these animals exerts an active retardation upon the rate of passage of water into the body. Marine Amphibia are unknown, and it is doubtful if any amphibian is capable of living in very concentrated salt solutions. When frogs are transferred to such solutions the osmotic pressure of the blood rises, due principally to increased concentration of salt, so that it remains osmotically superior to the external environment until lethal concentrations are reached (Δ = 0.6 to 0.8°C. Cf. Duval, '28). Until this time water absorption occurs along the existing osmotic gradient between the external medium and the body, and the urine remains hypotonic to the blood. The recent, naked skinned amphibia may possibly be secondarily aquatic, being derived from more terrestrial stegocephalian forms, and although there is

little reason to doubt that the physiological organization observed in them is significant in the interpretation of the evolution of the higher vertebrates no attempt can be made at this time to trace the successive steps of this evolution.

IV

It has been pointed out that it is the inability of the kidney to excrete a hypertonic urine that constitutes the central feature of the water and salt cycle in the fishes. In spite of this osmotic limitation, the fish kidney is fully competent in all all other respects. Both the elasmobranch and teleost kidney can excrete a very dilute urine and thus regulate the water content of the body when the organism is living in fresh water; and in either fresh or salt water the fish kidney can excrete salts and waste products (Na, K, Cl, Mg, Ca, SO_4, PO_4, urea, uric acid, creatine, creatinine, NH_4, etc.) in a manner entirely adequate to meet the needs of the organism. There is no justification for concluding, as some observers have done, (Margaria '30) that the fish kidney is incapable of performing its obvious duties.

It happens that in both the elasmobranch and the teleost a large proportion of the univalent salts and of ammonia are excreted extrarenally, but these are unquestionably physiological processes of great importance, and possibly of great antiquity, and must be interpreted in relation to the evolutionary history of the organism. It happens in both the elasmobranch and the teleost, that the greater part of the metabolic urea is excreted extrarenally (Smith '29b, '31a), probably by passive diffusion across the gills, but such a diffusion process seems to us to be inevitable considering the highly diffusible nature of this substance, and the thinness of the branchial respiratory membranes. In spite of these unusual circumstances, the fish kidney is capable of extraordinarily varied activity.

Its obvious deficiency, the incapacity to excrete a hypertonic urine, is not corrected, as we have remarked above, until the mammals or possibly the birds are reached. This deficiency appears to be a consequence of the evolutionary history of the vertebrates—a history which appears to be written quite legibly into both the anatomy and function of their chief excretory organ.

Beginning with the observations of Huot ('97) on the morphology of the kidney in the *Syngnathidae*, a number of fishes have been described which possess nearly or completely aglomerular kidneys (Marshall and Grafflin, '28; Marshall, '29). From our observations on the water equilibria in the marine teleosts we were led to suggest that the presence of glomeruli was a primitive character, and that their absence or degeneration in certain marine fishes was a specialization due to the decreased excretion of water relative to the fresh water ancestral stock (Smith '30a).

This suggestion was extended as a theory of the evolution of the vertebrate kidney by Marshall and Smith ('30). The evidence indicates that the provertebrate kidney was primitively aglomerular, and that it consisted of a series of tubules communicating with the coelom by means of nephrostomes, the tubules either opening separately to the exterior or into a common duct. It was postulated that the glomerulus was evolved in some early Palaeozoic fresh water chordate to enable the organism to excrete readily the large quantity of water which was absorbed along the osmotic gradient existing between its blood and its fresh water environment. This glomerulus represented simply an advantageous juxtaposition of the blood-vascular system to the already existing tubular system draining the (primi-

tively excretory) coelom. This postulate rests in part upon the function of the glomerulus as a filter, in accordance with current interpretations of renal function, and in part upon the palaeontological evidence that the Palaeozoic vertebrates lived in fresh-water, as reviewed in the first part of this paper.

So long as the organism remained in fresh water (dipnoans, ganoids, and teleosts) or in intimate dependence upon it (Amphibia), this excretory arrangement persisted; but with the secondary assumption of a marine habitat (teleosts) where the osmotic gradient was reversed and the water excretion reduced, or with the assumption of terrestrial life in which water conservation became a necessity (arid-living reptiles and birds), the organism no longer needed this primitive water-excreting mechanism, and could no longer use it economically. There was thus a need either (a) to discard or reduce the glomeruli or (b) to amend their primitive function by adding distally a more efficient mechanism for the reabsorption of water. The first process appears to be occurring in the fish, the birds and the reptiles; in the birds the central capillaries of the glomerular tuft are replaced by a dense core of syncytium-like tissue; in the reptiles the glomeruli are apparently being invaded by connective tissue (cf. Regaud and Policard ('03) and Cordier ('28)). While in the mammals on the other hand, and possibly to some extent in the birds, a further elaboration of the tubular portion (addition of the loop of Henle?) has permitted the reabsorption of water against the osmotic pressure of the metabolites and salts in the urine; consequently in these the glomeruli, although still very active as filters, have become secondarily incorporated into a filtration-reabsorption system which permits the excretion of waste products without the excretion of excessive quantities of water.

But the fate of the glomeruli is most striking in the marine fishes, in which all degrees of reduction, up to complete disappearance, may be observed. (For quantitative determinations of glomerular development in fish see Nash, '31; a few unpublished data of our own from the East Indies are included here.) Fresh water fishes have typically numerous and well developed glomeruli which contain many branched capillaries. Central euryhaline families, such as the perch, show moderate reduction in size and number of glomeruli. This process of glomerular reduction is not perceptibly furthered in the Labroidei, but it shows a marked advance in the Scorpaenoidei, in which the glomeruli are typically numerous but very small. The extreme of this reduction process is found in a few sub-orders.

Among the Blennioidei, for example, *Salarias faciatus* has very few, very small glomeruli, and in the Hoplodoci and Pediculati (*Opsanus*, *Batrachus*, *Lophius* and *Histrio*) the glomeruli have disappeared, the kidney remaining a purely tubular one. In the Hemibranchii, *Amphisile* has only a few small glomeruli and all the Syngnathidae so far examined (10 species) are aglomerular. This aglomerular condition persists in the fresh water pipe-fish, *Microphis boaja*, indicating that the structure of the kidney is a true phylogenetic character, and not a transient adaptation; for *M. boaja* is a derivative of the typically marine Syngnathidae, and must be considered to have secondarily invaded fresh water. Once gone, the glomeruli cannot be regained. Other aglomerular families include the Gobiesocidae and Saccopharyngidae.

It is not clear yet by just what intermediate steps the reduction of glomeruli

occurs. Grafflin ('29) found ninety-four glomeruli, each with a definite tubular connection, in an immature specimen of *Lophius*, but these apparently lose their connection with the tubules later for in the adult they are not only fewer in number but lack any connection with the renal tubules. Hence Marshall and Grafflin called them pseudoglomeruli.

The disappearance of glomeruli will, according to our interpretation, be influenced by the euryhaline or stenohaline habits of a fish, as well as by its present habitat, and it is therefore difficult to establish a detailed ecological explanation of glomerular development in various fishes. Like many other evolutionary specializations, the reduction of glomeruli probably proceeds slowly, and a more detailed paleontological history than is now available may be required in order to interpret the status of any one family, genus, or species.

V

From a chemical point of view it would appear that the regulation of the water content of the body by the extrarenal secretion of a hypertonic solution is no more efficient, and in fact probably less efficient, than the plausible alternative of extracting water directly from sea water. The former process requires a round-about cycle of enteric absorption of sea water and its salts, and results in placing an additional burden upon the gastrointestinal tract. It possesses the further disadvantage that considerable quantities of Mg and SO_4 are absorbed from the intestinal tract and these constitute an additional excretory burden upon the kidneys. Both these results might be avoided if water could be extracted from sea water directly by respiratory or integumentary membranes. The direct absorption of water, to the exclusion of salts, is apparently physiologically possible, for it is just such a process that we believe to occur in the renal tubules of mammals. The explanation of why the indirect method prevails in the teleosts (and primitively, we suppose, in the elasmobranchs) does not rest, apparently, upon any inherent advantage in the method but rather upon the evolutionary history of body fluid regulation.

If we suppose that throughout their evolution the vertebrates have been required for physiological reasons to maintain an approximately constant water content in their bodies, and if we further suppose that the theatre of this evolution has been largely in fresh water, then it would appear probable that the oldest regulatory mechanism in the body would be the organization of the respiratory and integumentary surfaces whereby exposed tissues controlled the ingress of water and the egress of salts. (The gills, for example, of fresh water fish are physiologically constructed to retain salt at a considerable level in the blood when their external surfaces are bathed with pure water. If we may use the terms loosely, we can say that they are physiologically orientated so as to be hypertonic to the external medium. The gills, of course, are the effective agent and not the blood which is only a remote and passive medium of circulation.) If the route of the extrarenal excretion of salts in the recent teleosts is the gills, as we have supposed, then this branchial excretion may be said to occur down the osmotic gradient established by this archaic, physiological orientation. If, when the fresh water ancestors of the present marine fishes migrated into the sea, the sea were more dilute than the blood then the osmotic relations would not be changed. But if the sea were more concentrated than the blood, or if it be-

came more concentrated with the passage of time, then it is to be expected that, in an effort to maintain the water equilibrium of the body, a progressively greater burden would be thrown upon the branchial membranes. These membranes, already oriented in the direction of hypertonicity with respect to the fresh water which had previously bathed them, would maintain this orientation and meet the new conditions in salt water by exalting their already existing functional operations. Thus, the marine fish, in secreting a hypertonic solution at the gills, may be continuing qualitatively in the mode of its fresh water ancestors, the only difference being an absolute elevation of the branchial osmotic level with respect to the blood.

This interpretation is purely speculative, but we have enlarged upon the point because it is important to recognize that the fundamental *modus operandi* of body fluid regulation in all the primitively aquatic vertebrates may be, according to the available facts, identical in nature; i.e., the extrarenal excretion of salt and the extrarenal control of osmotic pressure in both the fresh water and marine teleosts, and in the elasmobranchs as well, except as they have secondarily acquired their uremia mechanism, may be a very archaic operation evolved independently of any marine experience. It is interesting to note in this connection that Schlieper ('30), in his discussion of the regulation of the composition of the body fluids of invertebrates, lays emphasis upon the extrarenal regulation of osmotic pressure. Perhaps this operation in vertebrates is an homologous function.

In the most widely accepted theory of urine formation in mammals it is supposed that this process begins with the glomerular filtration of a protein-free fluid from the plasma; as this filtrate passes through the renal tubules, water is reabsorbed and waste products are thereby concentrated in the urine. This filtration-reabsorption process appears to be "going around your elbow to get to your thumb," since direct tubular excretion is possible, as is shown by the aglomerular fishes in which it does not appear to possess any great disadvantage (Marshall, '30). It would seem, according to our view, that the filtration-reabsorption system which exists in the mammals does not owe its existence to any great superiority of the method itself, but is again a consequence of the evolutionary history of the vertebrates. The kidney began, we suppose, as a nephrostomatous-secretion system in the marine provertebrate and became a filtration-secretion system in the early fresh water vertebrates; in the marine fishes (and perhaps in the reptiles and birds) it is reverting by loss of the filtering portion (glomeruli) to a simple secretion system, while in the mammals it is secondarily modified to a filtration-secretion-reabsorption system.

If the vertebrate kidney was evolved in a fresh water habitat, then not only the glomerular filter, but also the capacity to excrete a hypotonic urine may be viewed as a direct historical consequence of this fact; for it is just this type and only this type of excretory activity that would be needed under these conditions. Accepting at their face value the palaeontological interpretations of Chamberlain, Barrell and MacFarlane, we may suppose that it was as a highly evolved organ, and therefore bearing more or less indelibly this fresh water history, that the vertebrate kidney was carried into the sea or onto the land during Mesozoic time. It had never been called upon to perform hypertonic excretion since its definitive status was reached, and it never acquired this capacity until much later when, in the birds (?) and mammals, its further evolution occurred by the addition of a new portion

capable of absorbing water against osmotic pressure (loop of Henle?).

Although the fish kidney never acquired the capacity to excrete a hypertonic solution, its evolution was not arrested. Its primitive function has been significantly modified in the elasmobranch. When the teleost lives in the sea, it drinks sea water which it absorbs enterically, and subsequently excretes the bulk of the salt extrarenally, leaving water osmotically free for urine formation. The elasmobranch shows, in addition to this (primitive?) extrarenal mechanism, its physiological uremia which is effected principally by renal conservation. This uremia raises the osmotic pressure of the blood to a level above that of the surrounding sea water and enables the organism to absorb water directly, to the exclusion of salts, for the formation of its hypotonic urine. The uremia therefore makes it possible for the elasmobranch to escape the continuous drinking of sea water. The question arises whether or not the urea mechanism is a novel specialization in the elasmobranchs, or whether it is only the exaggerated activity of a mechanism which is common to them and to the teleosts, and perhaps to other vertebrates as well. Or it may represent a mechanism once important in the teleosts and other vertebrates, but now decadent or lost. In utilizing urea to aid in the absorption of water, the elasmobranch was only putting an old thing to a new use, but to do so it had to practice the apparently novel operation of renal conservation of urea—a substance which in other vertebrates is apparently only a waste product. It is an important principle that evolution usually progresses without abrupt changes in function, and this principle, if nothing else, would caution us against concluding that this operation, however novel it may appear, was a new or exclusive elasmobranch patent. But in addition to the altered activity of the kidney, the elasmobranchs had to render their branchial and oral membranes less permeable to urea in order to reduce the rate of diffusion of this substance out of the body, and in addition they had to resort to a viviparous habit (most Sharks, Dog-Fishes and Rays), or to invest the egg and embryo in a shell impermeable to urea (Scylliidae, Raiidae, etc.). In either case, they had to effect fertilization by internal impregnation. Since these specializations, which are apparently concomitants of urea retention, are collectively peculiar to the elasmobranchs, we are left with the feeling that the uremia mechanism is a specialization independently evolved by this Order of fishes. In any case, its evolutionary perfection must have antedated the separation of the Order into the Sub-orders Holocephali, Batoidei and Selachii, for these are all characterized by the uremic state.

VI

In conclusion, we may invert the view which we take of the above facts. We may construct a logical syllogism as follows:

As a major premise, we may take the evolutionary principle that functional adaptation corresponds to habitat; and as a minor premise we may take the physiological fact that the vertebrate kidney, from the elasmobranch up, is functionally sufficient to maintain the water equilibrium of the organism in fresh water, but functionally deficient, because of the absence of hypertonic excretion, to maintain this equilibrium in salt water or during terrestrial desiccation except as fresh water is ingested or as the kidney is further modified in the mammals.

1. Therefore the kidney must have acquired its *functional* nature in a *milieu* that was more dilute than the blood

(rather than in more concentrated sea water or on land).

To this we may add a second syllogism using for our major premise the principle that morphological adaptation corresponds to habitat; and for our minor premise the fact that the renal glomerulus is best developed in fresh water teleosts and Amphibia, and tends to degenerate in the reptiles and birds and to undergo complete extinction in the highly specialized marine fishes.

2. Therefore the kidney must have acquired its *glomerular* character in a *milieu* that was more dilute than the blood.

Or we can construct a third syllogism, using the same major premise as in (1) but substituting for our minor premise the fact that:

The recent elasmobranchs approach the recent teleosts in respect to the composition of the blood and the mode of its regulation when both are inhabitants of *fresh water*; (these forms acquire a different composition and a different mode of regulation when they are inhabitants of sea water).

3. Therefore both must have had a common phyletic history in a relatively dilute *milieu* at some remote and predefinitive stage.

Superficially, then, the above facts point very strongly to a fresh water history for the early vertebrates. But it will be noted that the first two deductions hinge upon the relative osmotic pressure of the *milieu intérieur* and *milieu extérieur* during the formative period of the kidney. Their significance would be greatly diminished if it could be shown that the Palaeozoic seas were more dilute than the blood of the contemporary vertebrates. It would seem, according to the conservative interpretations of geologists, that the salinity of sea water has been increasing more or less steadily ever since the oceans were formed some 1500 million years ago; by proportion then, the seas of earliest Palaeozoic times should have had at least two thirds of the osmotic pressure of the present oceans, or a Δ of 1.3°C. The continental waters, on the other hand, have probably always been dilute (Δ = 0.1 to 0.2°C.).

But we do not know what the osmotic pressure of the blood of the Palaeozoic forms was, and we dare make no assumptions on the matter because these forms may have been derived from a marine invertebrate that was hypertonic to the contemporary sea water, as many invertebrates are today, and therefore they may have been *functionally hypertonic to the sea water in which they lived*, as are the recent elasmobranchs and *Myxine*. It does not seem likely, however, that this slight degree of hypertonicity would suffice to impress upon them such distinctive characters as we have noted above, but more information is needed on this point before any definite conclusion can be drawn. For the present, the most we can say is that the physiological and anatomical characters of the fish kidney are most easily interpreted on the assumption that the Palaeozoic vertebrates were inhabitants of fresh water at the time when these characters were laid down.

SUMMARY

The kidneys of apparently all vertebrates from the elasmobranch fishes to the birds and mammals are capable of excreting a very dilute or hypotonic urine when the animal is living in, or ingesting fresh water. It is only in the mammals or possibly in the birds that the capacity to excrete a urine significantly hypertonic to the blood appears; this capacity may be

attributable to the loop of Henle in the renal tubules of the higher forms.

In the fresh water teleosts and elasmobranchs the extensive absorption of water which occurs along the osmotic gradient between the external medium and the body is effectively offset by the continuous excretion of abundant hypotonic urine, and at the same time waste products are eliminated from the body in this abundant urine.

When the organism lives in sea water, there is not only a constant tendency for water to be lost from the body as a result of osmotic extraction, but the osmotic limitations of the kidney require that water be separated from the relatively concentrated external medium, in order to permit the formation of a dilute urine for the excretion of waste products.

The marine teleost solves this problem by drinking sea water and absorbing most of the water and salt from the gastro-intestinal tract; after which the salt is largely excreted by some extrarenal route (probably the gills) so that water is left osmotically free for urine formation.

The marine elasmobranch resembles the teleost in its ability to excrete salts extrarenally; but in addition to this primitive process the elasmobranch resorts to a secondary mechanism in the form of a physiological uremia, which enables it to absorb water directly. Urea is an end product of protein combustion in the elasmobranch, as in the dipnoan, the teleost, the Amphibia and the mammal, but a functional uremia is established by the simple expedient of conserving this substance at the kidneys (presumably by reabsorbing it from the glomerular filtrate) and at the same time the permeability of the gills, the oral membranes and the integument to urea is so diminished that its diffusion from the body is greatly reduced. The urea consequently accumulates in the blood (to the extent of 2.0 to 2.5 per cent) until the total osmotic pressure rises above that of the external medium, when water can be again absorbed directly by the external membranes. The elasmobranch is thus freed of the necessity of continually drinking sea water.

Thus water absorption, water excretion (as urine) and the water content of the body become directly dependent in the elasmobranch upon the renal conservation (or excretion) of urea. This physiological uremia tends to persist, though at a much lower level, in elasmobranchs which have secondarily invaded fresh water.

The essential features in the evolution of body-fluid regulation throughout the vertebrates appear to be the maintenance of, first, a constant water content and second, a constant salt content in the body. A comparison of the elasmobranchs with the teleosts indicates that the constancy of the osmotic pressure in the blood and body fluids of the latter is an incidental result of the simultaneous regulation of water and salt content, and that the osmotic pressure, *per se*, is not physiologically significant.

There is some palaeontological evidence that the first fishes primitively inhabited fresh water. It is suggested here that the *hypotonic limitations* of the kidney in the lower vertebrates, the *glomerular nature* of the renal unit in the primitive fishes and the *physiological similarity* between the elasmobranchs and the teleosts when in fresh water, are most easily interpreted on the assumption that the early vertebrates were inhabitants of fresh water at the time when the definitive character of the vertebrate kidney was established.

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ECOLOGY OF POPULATIONS

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THE PROBLEM

THE study of populations of late years has acquired a particular interest. A great stimulus to the work along this line has been given by the discovery of the law of population growth made by Raymond Pearl.

"A population may be defined as an aggregation of individual organisms of the same species, living together in a limited and defined universe" (28, p. 515). In the case of human population it is the population of a town or of a country that possesses these characters. As an example of population among insects we can take a group of grasshoppers of a certain species inhabiting a given locality. The density of such a population may be considered as its most important characteristic. It can be expressed by the number of individuals occupying a certain unit of space. In field ecology this notion is designated as the abundance of a species. For terrestrial animals like grasshoppers the density of population may be expressed by the number of grasshoppers dwelling on the space of one square meter.

The density of population is very important because of its influence on the trend of the main biological processes. Raymond Pearl has shown that it has a pronounced influence on the longevity and fertility of organisms. The rate of growth is also connected with the density of population, which in its turn depends on different factors of environment. We observe it on examining the distribution of organisms in natural conditions. Every organism occupies usually a definite vital zone with most favorable conditions. At the same time, according to field investigations, the density of population of a given species is not the same in different parts of its vital zone. The density of population reaches its highest value in definite optimal conditions, decreasing in such habitats where the conditions deviate from the optimum. The study of the correlation between the density of population and environment represents the leading problem of the ecology of populations.

Field investigation is one of the methods for such a study. It requires a detailed examination, on the one hand, of the environment in which a given organism dwells, and on the other, of the density of population of this organism under different conditions of environment. Unfortunately the relationships existing in nature are not easy to elucidate. First of all, we are dealing here, not with separate physico-chemical and social factors of environment, but with their combinations, which are variable in time. Moreover it is often rather difficult to obtain accurate determinations of the population size and of the factors of environment. All this brings us to the necessity of an experimental study of the influence of ecological factors on the density of population.

As an example of such an experiment we can take the growth of population of a species of insect under different temperatures. For this purpose jars equal in shape and size are filled with the same quantity of food, each populated by a pair of insects, one male and one female, and kept

in the thermostats at different temperatures (all other conditions being identical in all jars). To bring the conditions of the experiment as close as possible to those of nature, fresh food must be supplied at fixed intervals. Every pair placed in a jar will produce its progeny, this generation will produce another, and the population will go on increasing until it reaches an asymptotic value, saturating the given microcosm. Experience shows that the level of this asymptotic population will be different at different temperatures. The dimension of the microcosm being the same at different temperatures, the level of the asymptotic population can be considered as the density of saturating population, if we take our microcosm as a unit of space. On the basis of the experimental data obtained, the relationship between the density of population and temperature can be expressed in mathematical terms by means of an equation.

The populations in such experiments differ from those in nature in two points. Firstly, in field conditions a whole complex of factors influences the population, whereas in the experiment we are dealing with only one factor. Secondly, in the experiment we are analyzing the density of saturating populations, whilst in nature the conditions are continually changing and we meet saturating as well as nonsaturating populations. Extended observations can decide whether a given population is saturated or not. The only exact data available are those concerning human populations. These data show that in one country the population may be almost saturated, undergoing at the same time a process of rapid growth in a neighboring one. It may be supposed that among animals the population can reach its asymptotic value in one habitat and be far below it in another.

The considerations just brought up show clearly that the relationships between the density of population and environment in natural conditions are very complicated, and that the experimental method helps us to simplify them. It is to be hoped that both methods taken together will solve many problems of the ecology of populations. The purpose of the present paper is to summarize the results of the observations and experiments of the author. Most of the material appears here for the first time.

DENSITY OF POPULATION IN NATURAL CONDITIONS

Convenient material for the field study of the ecology of populations is presented by the Orthoptera. I investigated in the North Caucasus the distribution of the Orthoptera in relation to their habitats during two summers. The results obtained in 1928 have been already published (12). This section presents the material obtained in 1929.

Orthoptera dwell in very different habitats and the distribution of separate species is closely connected with ecological factors. A series of papers on the ecology of these insects show that the vegetable cover is for them an ecological factor of the utmost importance (40, 44). At the same time the majority of species of Orthoptera are not monophagous, and their food is not restricted to any particular kind of plant. Therefore in the choice of the habitat the composition of the vegetable covering is not of essential importance. What is essential is the density of this cover, on which the microclimate of the habitat depends in a great measure. Thus, for instance, where there is a dense cover of vegetation (all other conditions being equal), the relative humidity of the air is greater, and the temperature lower than in the habitats with a scanty vege-

tation, where the soil gets more heated and the vegetable cover is better aerated.

The microclimate is very important for the Orthoptera and we can evaluate exactly separate factors, whose union constitutes the microclimate. The most important among them are: temperature, relative humidity and evaporation power of the air. The total effect of air temperature, pressure, relative humidity, and average wind velocity upon a free water surface is expressed by the amount of water evaporated. The same factors have been shown to determine the amount of evaporation from the bodies of organisms.

TABLE 1

Microclimatical characteristics of the habitats studied

NUMBER OF HABITAT	TEMPERATURE	RELATIVE HUMIDITY IN PER CENT	EVAPORATION PER HOUR
1	49.5	62.7	363.3
2	48.1	64.0	300.0
3	44.1	65.8	276.5
4	45.5	65.3	274.2
5	34.8	67.8	187.2
6	41.8	66.7	235.1
7	40.9	66.6	214.5
8	33.8	69.5	202.8
9	33.2	71.7	181.5

Table 1 presents the microclimatic characteristics of nine habitats studied in the Mazesta river valley (North Caucasus). The data of this table are the average data of two groups of determinations made at the end of August and the beginning of September, 1929, the results of which were analogous. The determinations were made at noon. In every habitat the temperature was taken with the aid of two different thermometers, the relative humidity with the Saussure hygrometer, and evaporation with a quick-reading atmometer, resembling in its construction the one described by Wilson (45). It must be borne in mind that the evaporating surface of our apparatus differed from Livingston's standard spherical atmometer both in size and shape, and that the data in table 1 are expressed in the units of our apparatus and not in cubic centimeters. Figure 1 represents graphically the data of table 1. Separate habitats differ somewhat sharply in their main microclimatical factors. At the same time a close connection exists between these factors. For instance, a rise of temperature in the habitat is accompanied by an increased evaporation and a decrease of relative humidity. We can consider each one of these factors

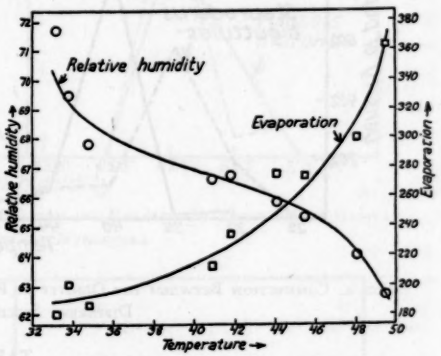

FIG. 1. CONNECTION BETWEEN THE TEMPERATURE, RELATIVE HUMIDITY, AND EVAPORATION IN THE HABITATS OF THE ORTHOPTERA

Circles and squares represent the separate habitats

as an indicator, which reflects more or less the alterations of the entire microclimatical complex.

Together with the measurement of the environmental factors, we must evaluate the density of population of separate species in different conditions of environment. The direct determination of the number of individuals on the space of one square meter is here very difficult, and it is necessary to adopt methods enabling us to find equivalent values. The "*Zeitfänge*" method, successfully applied by Herold (18, 19), is good for our purpose. It consists in collecting all the Orthoptera of

the given habitat during a fixed time (in our case fifteen minutes) and counting the number of individuals taken. The number of individuals of the given species taken within the fifteen minutes is considered as the density of population of this species. Taking certain precautions (12) and calculating means on the basis of a series of observations, this method will give us in general satisfactory results.

The data thus obtained can be used for studying the connection between the density of population and the microclimatical factors. Figure 2 gives in the form of curves the connection between the density of population and temperature in different species of Orthoptera. These curves have been constructed in the following manner: the nine habitats studied have been distributed on the temperature scale; for each class of the scale average density of population has been calculated, and the data obtained have been expressed as percents (the sum of the average densities of all the classes being taken as 100). In every case the imago and the larvae have both been

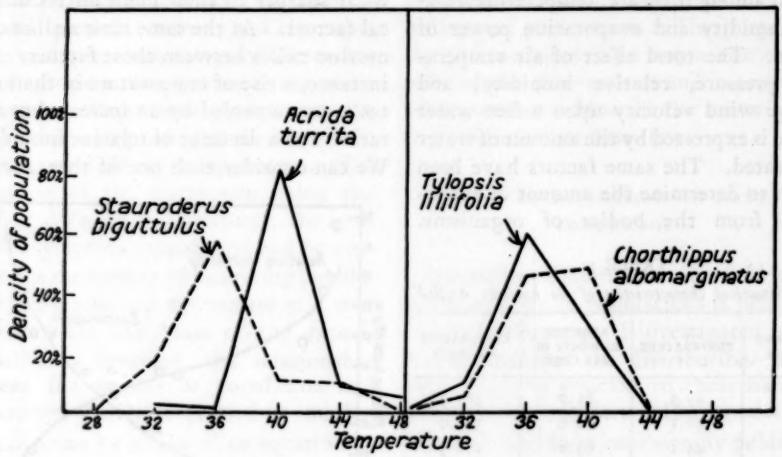

FIG. 2. CONNECTION BETWEEN THE DENSITY OF POPULATION AND TEMPERATURE OF THE HABITAT IN DIFFERENT SPECIES OF ORTHOPTERA

TABLE 2

The connection between the density of population and temperature, relative humidity and evaporation of the habitats in different species of Orthoptera

	NUMBER OF INDIVIDUALS	TEMPERATURE					RELATIVE HUMIDITY IN PER CENT					EVAPORATION PER HOUR				
		32°	36°	40°	44°	48°	63.5	65.5	67.5	69.5	71.5	190	230	270	310	350
1. *Acrida turrita*.....	201	3.2	1.4	82.0	9.0	4.4	6.1	11.9	73.4	5.2	3.4	2.5	79.6	8.9	7.7	1.3
2. *Stauroderus biguttulus*....	74	18.8	58.5	11.3	10.5	0.9	1.2	13.6	35.8	12.3	37.1	57.6	20.3	18.7	3.4	—
3. *Stauroderus macrocerus*....	168	4.1	—	95.9	—	—	—	—	88.7	11.3	—	2.5	97.5	—	—	—
4. *Tylopsis liliifolia*.....	40	10.0	60.0	30.0	—	—	—	—	66.0	34.0	—	46.5	53.5	—	—	—
5. *Chorthippus albomarginatus*.....	84	5.1	46.2	48.7	—	—	—	—	82.1	6.7	11.2	35.7	64.3	—	—	—

taken into account. The corresponding numerical material is given in table 2.

We can see from these curves that in certain optimal conditions the density of population attains its greatest value, which decreases as the conditions deviate from the optimum. Figures 3 and 4 represent the connection between the density of population and relative humidity, and density of population and evaporation, which have the same form. As already remarked, each of these factors can be

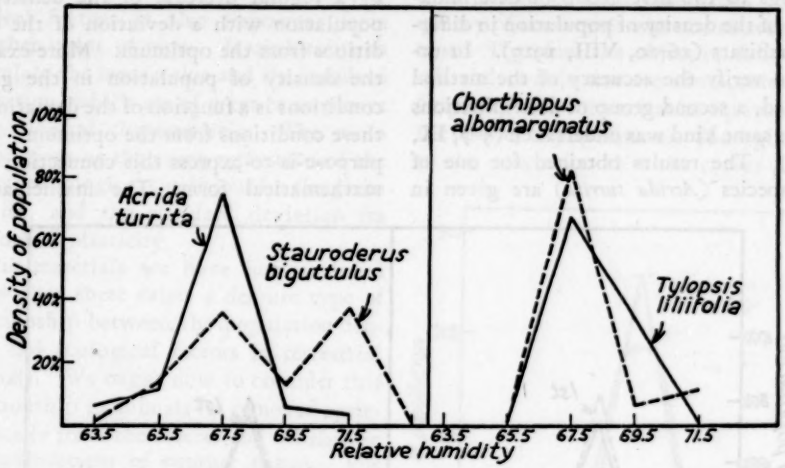

FIG. 3. CONNECTION BETWEEN THE DENSITY OF POPULATION AND RELATIVE HUMIDITY OF THE HABITAT IN DIFFERENT SPECIES OF ORTHOPTERA

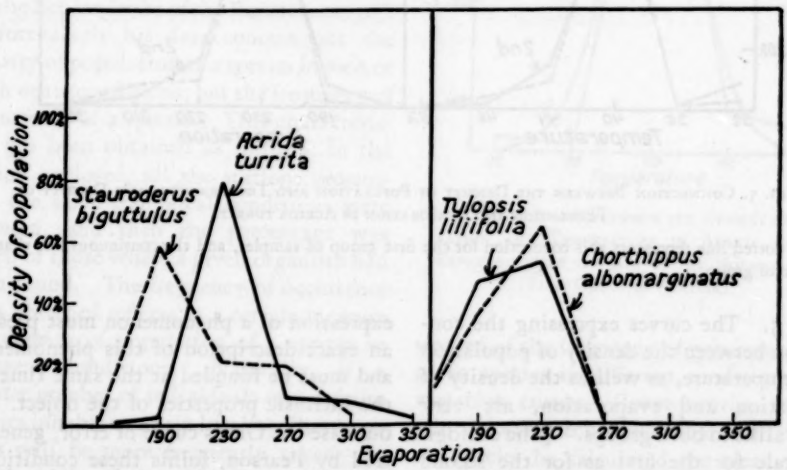

FIG. 4. CONNECTION BETWEEN THE DENSITY OF POPULATION AND EVAPORATION OF THE HABITAT IN DIFFERENT SPECIES OF ORTHOPTERA

considered as an indicator of the alteration of the entire microclimatic complex.

The material we have so far analyzed belongs to the first group of determinations of the density of population in different habitats (16–20, VIII, 1929). In order to verify the accuracy of the method applied, a second group of determinations of the same kind was undertaken (5–7, IX, 1929). The results obtained for one of the species (*Acrida turrita*) are given in figure 5. The curves expressing the connection between the density of population and temperature, as well as the density of population and evaporation, are very much alike in both groups. (The ecological scale for the first as for the second group has been drawn up on the basis of the average microclimatical characteristics of the habitats; see table 1.) This shows that the methods we have used are sufficiently exact.

Let us now consider more closely the curves expressing the correlation between the population density and the ecological factors. These curves are characterized by a regular decrease of the density of population with a deviation of the conditions from the optimum. More exactly the density of population in the given conditions is a function of the deviation of these conditions from the optimum. Our purpose is to express this connection in a mathematical form. The mathematical expression of a phenomenon must present an exact description of this phenomenon and must be founded at the same time on the intrinsic properties of the object. In our case the Gauss curve of error, generalized by Pearson, fulfils these conditions. Figure 6 represents the connection between the density of population and temperature in *Acrida turrita*, expressed with the aid of the normal curve. This function describes accurately the relationship under consideration, and with the differ-

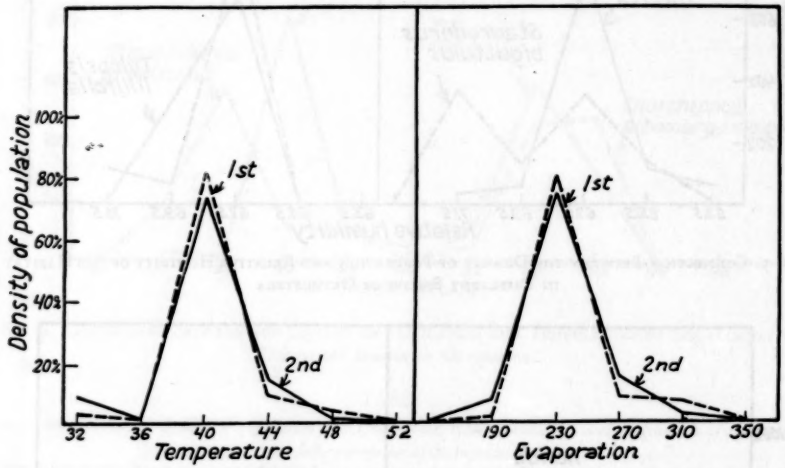

FIG. 5. CONNECTION BETWEEN THE DENSITY OF POPULATION AND TEMPERATURE, AND DENSITY OF POPULATION AND EVAPORATION IN ACRIDA TURRITA

The dotted line represents this connection for the first group of samples, and the continuous line that for the second group.

ent abscissae we obtain the values of the ordinates, possessing a real biological significance. The given type of connection between population density and ecological factors is also important from another point of view. It enables us to calculate the mean value and the standard deviation, which are of great consequence as ecological characteristics. The mean value gives us the exact expression of the average ecological conditions for the given species, and the standard deviation its ecological plasticity.

The materials we have just analyzed show that there exists a definite type of relationship between the population density and ecological factors in terrestrial animals. We ought now to consider this relationship in animals far removed systematically from the insects and inhabiting an environment of another nature. For this purpose we can utilize the material obtained by Shorygin in his study on ecology of the Echinoderms of the Barents sea (36). Unfortunately his data concern not the density of population of a species in such or such other conditions, but the frequency of occurrence of a species. This characteristic has been obtained as follows: in the region explored, all the stations presenting the same ecological conditions were counted, and then the percentage was given of those where a given organism had been found. The frequency of occurrence thus obtained reflects in a certain measure the density of population of a species in different conditions. Naturally, if a greater number of individuals of a definite species inhabit a certain locality, these animals will be more frequently taken. It may be objected that when the density of population of a species has attained a certain degree, individuals of this species will always come up in the bottom sampler, and the further increase of the population density cannot be evaluated. But among the species studied by Shorygin the one occurring most frequently was found in only about 50 per cent of the stations, and even under optimal conditions its frequency of occurrence was not above 76 per cent. Therefore the objection falls of itself and in this case we can consider the frequency of occurrence as an equivalent to the density of population. Shorygin came to the conclusion that the curves he has

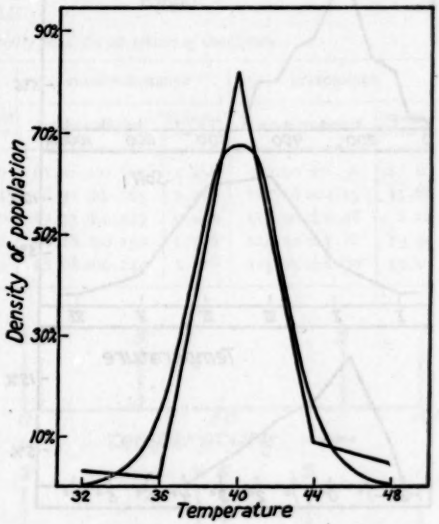

FIG. 6. CONNECTION BETWEEN THE DENSITY OF POPULATION AND TEMPERATURE IN ACRIDA TURRITA, EXPRESSED WITH THE AID OF THE NORMAL CURVE (FIRST GROUP OF SAMPLES)

studied of the frequency of occurrence of a given species in different conditions, are variation curves. Consequently, to obtain the exact ecological characteristic of the species he calculated the mean value and the standard deviation of these curves. Several curves from the work of Shorygin are reproduced in figure 7. These curves show the connection between the frequency of occurrence of the starfish *Asterias panopla* and the depth of its habitat,

the type of soil and the temperature. These curves allow us to conclude that the greatest density of population exists within certain optimal conditions and decreases regularly when the conditions deviate from the optimum. It is evident that the type of connection between population density and the ecological factors is on the whole the same, whether it concerns the echinoderms of the Barents sea or the Orthoptera.

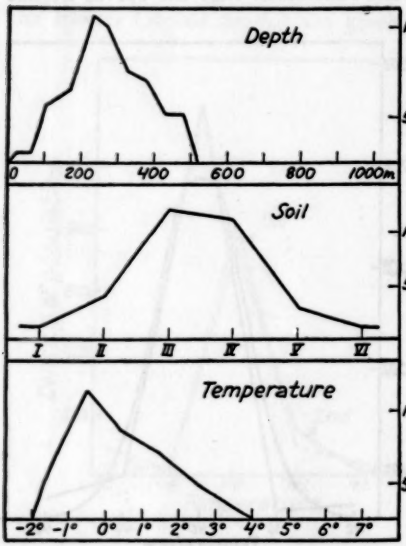

FIG. 7. CONNECTION BETWEEN THE FREQUENCY OF OCCURRENCE OF THE STARFISH ASTERIAS PANOPLA AND THE DEPTH OF ITS HABITAT, THE TYPE OF SOIL AND THE TEMPERATURE

(From Shorygin, 1928)

We have had in view here the connection between the density of population and the so-called significant variables of the environment. Allen gives for them the following definition (2, p. 225):

> There are some features or combinations of features in every environment which visibly affect its aspect with respect to particular organisms. . . . . Whether these operate directly to induce changes in aspect or whether they operate through resultant or coördinate relationship with other features, they may serve a useful purpose as vulnerable points for attack in practical studies of relationships within the environment. They may be regarded as *significant* variables in the environment.

The analysis of the material at our disposal has led us to conclude that the relationship between the density of population and the significant variables of environment in natural conditions can be expressed in a mathematical form by means of the Gauss curve, generalized by Pearson. This nevertheless does not shed any light on the question as to the causes responsible for this type of connection and does not allow us to admit the similarity of a given phenomenon with others, simply on the ground of their being described by the same mathematical function. Raymond Pearl writes (24, p. 558–559):

> The literature of science shows nothing clearer than that the same type of curve frequently serves to describe with complete accuracy the quantitative relations of widely different natural phenomena. As a consequence any proposition to conclude that two sets of phenomena are causally or in any other way fundamentally related solely because they are described by the same type of curve is of very doubtful validity. . . . . If there is good evidence *on other than quantitative grounds* that two sets of phenomena are qualitatively alike it is pertinent and significant to present as additional and confirmatory evidence data tending to show that these sets of phenomena are similar in their quantitative relations.

Our analysis must stop here, as the material we have in hand is insufficient to explain the causes of the type of connection we have established. One of the ways of elucidating this question is an experimental study of the influence of the separate ecological factors on the density of saturating population. It will be considered later.

ECOLOGICAL CHARACTERISTICS

The calculation of the mean value of our ecological curve permits us to evaluate

the average ecological conditions of a given species from an absolutely objective point of view. This is particularly important as regards the comparative study of the ecology of separate species. Also the possibility of calculating the standard error of the mean value facilitates the comparison of the average conditions belonging to different species. On table 3 we find the mean values together with their standard errors in the column "Average conditions." Figure 8 shows the distribution of the average conditions of the species studied, on the ecological scale of temperature, relative humidity and evaporation. To facilitate the comparison of different species, the distance between the average conditions of the extreme species is taken as 100. Considering figure 8 we can say that every ecological factor presents its own system of similarities between different species. For example, species 2 and 4 are very much alike in their average temperature conditions, whereas species 5 is further removed. If we consider next the average conditions of relative humidity, it will appear that species 4 and 5 stand close together, being far removed from species 2. This is due to the fact that each of the factors we have studied reflects more or less the alteration of the entire microclimatic complex and that by using different indicators the results we reach are different.

TABLE 3

Average conditions and ecological plasticity for different species of Orthoptera

	TEMPERATURE		RELATIVE HUMIDITY		EVAPORATION	
	Average conditions	Ecological plasticity	Average conditions	Ecological plasticity	Average conditions	Ecological plasticity
1. *Acrida turrita*.....	40.40 ±0.176	2.500	67.26 ±0.103	1.456	240.20 ±1.96	27.80
2. *Stauroderus biguttulus*.....	36.65 ±0.409	3.524	68.91 ±0.265	2.280	217.16 ±4.15	35.68
3. *Stauroderus macrocerus*.....	39.67 ±0.123	1.600	67.73 ±0.049	0.632	229.00 ±0.48	6.20
4. *Tylopsis liliifolia*.....	36.80 ±0.380	2.400	68.18 ±0.150	0.946	211.40 ±3.16	19.92
5. *Chorthippus albomarginatus*..	37.74 ±0.257	2.360	68.08 ±0.144	1.318	215.72 ±2.09	19.20

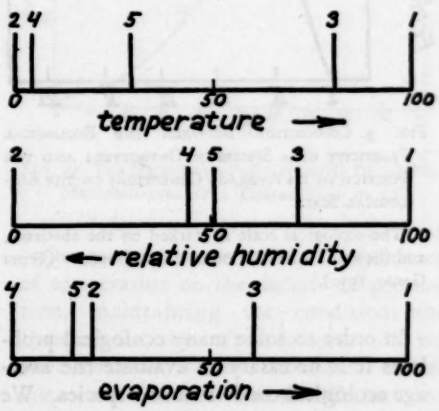

FIG. 8. THE DISTRIBUTION ON THE ECOLOGICAL SCALE OF THE AVERAGE CONDITIONS OF THE SPECIES OF ORTHOPTERA STUDIED

The ecologist must not restrict himself to the study of isolated "factors," but consider the microclimatic complex as a system presenting a whole. The problem of exact characterization is of the utmost importance, and in this respect ecological methods ought to be analogous to those which are finding their application in the field of mathematical morphology. Recently Eugen Smirnov has formulated the problems of this science (37). While studying the correlations between the characters of an organism, we see that some of them are more important, and others less. A character closely connected

with many others is of greater importance for characterization than one with fewer connections. The former is an indicator allowing us to discern the presence of others. In this manner if we possess a great number of indicators, and if we know their correlations, we are able to represent to ourselves the organism as a whole. It is known that in statistics a series of methods have been elaborated facilitating the choice of such indicators. These methods can be used for the study of microclimatic complexes as well.

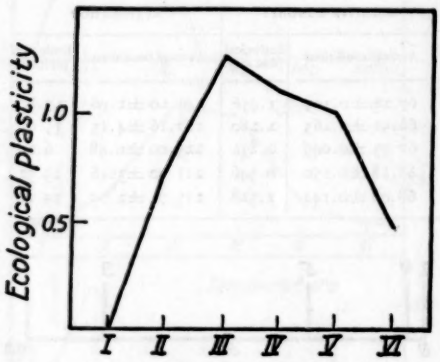

FIG. 9. CONNECTION BETWEEN THE ECOLOGICAL PLASTICITY OF A SPECIES OF ORTHOPTERA AND THE POSITION OF ITS AVERAGE CONDITIONS ON THE ECOLOGICAL SCALE

The ecological scale is marked on the abscissae, and the standard deviation on the ordinates. (From Gause, 1930).

In order to solve many ecological problems it is necessary to evaluate the average ecological conditions of a species. We mean the exact study of the alterations of the average conditions as regards time. But up to the present this question has scarcely been touched upon.

Another important ecological characteristic is the standard deviation, which reflects the ecological plasticity of a species. It gives the means of evaluating not only the ecological amplitude of a species, but likewise the concentration of its population in respect to the average conditions. If, with a slight deviation from the average conditions of a species, the density of its population decreases considerably, this species is not so plastic as another one, in which the same deviation from average conditions produces but a very small decrease of population density. The standard deviation enables us to evaluate exactly these differences in plasticity.

The data on the ecological plasticity of several species of Orthoptera are given on table 3. Rather sharp differences exist between separate species. To illustrate the application of this characteristic to ecology, we will consider an example taken from our previous paper (12). We have investigated the ecological plasticity of fifteen species of Orthoptera in connection with the position of the average conditions of these species on the ecological scale. The relationship found can be seen on figure 9. The ecological scale is marked on the abscissae, and on the ordinates for each class of this scale is given the average ecological plasticity of the species, whose average conditions range them in a given class. Figure 9 enables us to affirm that the species for which extreme habitats, dry ones (class I) as well as moist ones (class VI) constitute average conditions, possess only a slight ecological plasticity. At the same time the further the average conditions of a given species are removed from the center to the periphery the less is its ecological plasticity. All these correlations are based on the study of a comparatively small group of Orthoptera consisting of 15 species. It remains for future investigations to show how wide is the extension of these regularities.

THE INFLUENCE OF TEMPERATURE ON THE DENSITY OF POPULATION OF DROSOPHILA

The next step in studying the ecology of populations is the experimental investiga-

tion of the influence of separate ecological factors on the density of saturating population. The choice of the object for investigation is here of the highest importance. It must answer to the following requirements: (1) it must develop rapidly so that in a short space of time a great number of experiments could be set and verified, (2) the determinations of the density of population at fixed intervals of time must not encounter any technical difficulties, so as to ensure the obtaining of average data from numerous separate determinations, and (3) the technical difficulties for breeding a given organism must be reduced to a minimum.

In the winter of 1929–1930 I made several experiments on the influence of temperature on the growth of population of the fruit-fly *Drosophila melanogaster*. However, this insect does not completely satisfy the requirements (2) and (3). Raymond Pearl has recently discussed in detail the numerous difficulties arising in the course of an experimental study of population growth in *Drosophila*. Various microorganisms are more convenient for our purpose. Biologically these populations are the most simple and usually they fulfill completely the conditions specified above. It has been recently pointed out by Bail (3) that bacteria can be successfully used for an experimental population study. A series of papers by Richards (30, 31, 32, 33) leaves no doubt as to yeast furnishing one of the most appropriate materials for such investigations. I worked experimentally upon yeast in the winter 1930–1931, and the results obtained are given in the next section.

For the experimental study of population growth, *Drosophila melanogaster* was first used by Raymond Pearl. He worked out the technique of experimentation which is described in his book *The Biology of Population Growth*. Pearl came to the conclusion that the so-called symmetrical logistic curve can be taken as the mathematical expression of the growth of population of *Drosophila*. Such a curve is represented in figure 10. It shows that the population increases regularly until it reaches a certain asymptotic value, saturating the given microcosm. It has been found by Pearl (25) that in microcosms equal as to volume and quantity of food, the levels of saturating populations of different races are different. Consequently racial differences have much to do with determining the final asymptotes approached.

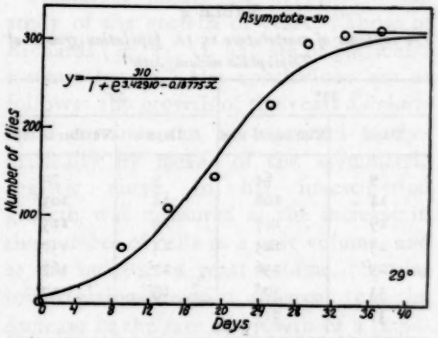

FIG. 10. THE GROWTH OF POPULATION OF DROSOPHILA MELANOGASTER AT A TEMPERATURE OF 29°

Our purpose was to study the influence of temperature on the density of population, maintaining the conditions unchanged for the other factors. As we have remarked already, the volume of the microcosm was the same at different temperatures and in our case the level of asymptotic population may be considered as the density of saturating population if we take our microcosm as a unit of space. Two series of experiments at different temperatures were made. We give here the results of two experiments of the second series. The material consisted of young flies belonging to race 107 and hatched from the pupae three days before. This

race had been brought by Dr. W. W. Alpatov from the Institute for Biological Research (Baltimore). A pair of flies was placed in a bottle of about 200 cc. in volume. Up to the depth of 1.5 cm. the bottle was filled with potato-raisin food, over which liquid yeast, constituting the principal food of *Drosophila*, was spread. The wide neck of the bottle was closed by a cotton wool stopper. While the experiment was going on, a small quantity of food was added twice; also a few drops of distilled water were introduced at regular intervals. The number of flies in the bottle was counted from time to time in the following manner: A wide test tube strongly lighted was introduced into the neck of the bottle, and the flies, attracted by the light, crawled into it. The few flies remaining in the bottle were gently shaken out into the tube. After this the flies in the test tube were slightly etherized, counted rapidly and put back into the tube. They were left there for a short time, and only when they had completely revived were they replaced in their bottle.

TABLE 4

The influence of temperature on the population growth of Drosophila melanogaster

29°		30°	
Days	Number of flies	Days	Number of flies
9	64	9	70
14	108	14	103
19	145	19	123
25	225	24	137
29	296	27	167
33	308	29	127
37	311		
Asymptote = 310		Asymptote = 146	

Table 4 gives the data on the growth of population of *Drosophila* at temperatures of 29° and 30°. In both cases thermostats with electrical heating were employed and the temperature records show that the average temperature in the first case was 28.95° and in the second 29.98°. Four bottles were kept at each of these temperatures and the number of flies given in table 4 represents the average data. In figures 10 and 11 this material is represented graphically and the equations of the fitted logistic curves are given.

The most interesting feature for us is the asymptotic population. Our data made it evident that temperature has a pronounced influence on its level. Thus at a temperature of 29° the asymptotic population is 310 flies per bottle, and at 30° it is only 146 flies. Such a sharp difference is probably due to the fact that this part of the temperature scale is a critical one for *Drosophila*. It has been shown by Crozier (9) that the temperature of 30° is accompanied by critical effects in various kinds of vital activities. As regards *Drosophila* we can mention Bliss (5), who found that a temperature above 30° delays the prepupal development, and Young and Plough (46), who showed that a temperature of 31° produces the sterilisation of the males of *Drosophila*.

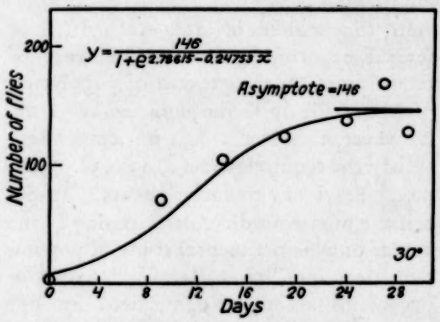

FIG. 11. THE GROWTH OF POPULATION OF DROSOPHILA MELANOGASTER AT A TEMPERATURE OF 30°

Our data on the influence of temperature on the density of saturating population of *Drosophila* agree completely with those

published by Arata Terao. This author studied the influence of temperature on the growth of population of the water-flea *Moina macrocopa* and came to the conclusion that the temperature influences the level of saturating population.

The principal point to be considered is the mathematical expression of the relationship between the density of population and temperature. We attempted to express mathematically some of the data published by Terao (14). In figure 12 the connection between the level of asymptotic population of *Moina* and temperature is represented in the form of a curve. The volume of the microcosm and the quantity of food were the same at the different temperatures. It is evident that in certain optimal temperature conditions the density of saturating population is at its highest, diminishing as the conditions deviate from the optimum. It appears that the normal curve can be used for expressing the experimental data, but the number of the points obtained from experimentation is so far unsufficient. This question requires further investigation.

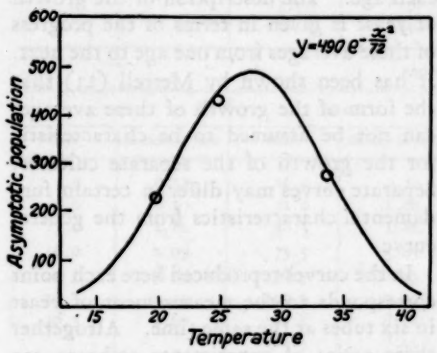

FIG. 12. THE INFLUENCE OF TEMPERATURE ON THE LEVEL OF ASYMPTOTIC POPULATION OF THE WATER-FLEA MOINA MACROCOPA ACCORDING TO THE EXPERIMENTAL DATA PUBLISHED BY TERAO

(From Gause, 1931)

YEAST POPULATION

Yeast cultures represent an excellent material for the experimental study of populations. Our purpose was to answer the following question: does the temperature influence the density of saturating population of the yeast? Would the population growth be slow at low temperatures, but ultimately reach the same level as in optimal conditions? In case the temperature does influence the density of saturating population, what will be the mathematical expression of the correlation between the density of population and temperature?

Numerous papers are devoted to the study of the growth of yeast. Those of Richards (30, 31, 32, 33) are of particular interest for us. His conclusions are as follows: the growth of the yeast *Saccharomyces cerevisiae* can be expressed mathematically by means of the asymmetric logistic curve. In his investigation growth was measured as the increase in the number of cells in a unit volume, and as the increase of yeast volume. Special investigations made it apparent that the decrease in the rate of growth of a population of yeast cells and its approach to the asymptotic value are due to the substances excreted into the culture medium by the growing cells. Alcohol is the product which primarily causes the decline of the growth rate. When the medium is maintained effectively constant by preventing the accumulation of these toxic products, the yeast growth is potentially unlimited. Toxic substances injure the buds, as the percentage of budding cells is about the same at the time of the most rapid growth and at the time of equilibrium, when the population attains the asymptotic level. In the early stages of the growth of yeast population the size of all the cells is nearly the same. But it is the largest buds that are selectively in-

jured by the toxic substances. They evidently are destroyed as soon as they become independent of the mother cell, and then the population consists of large resistant cells to which small buds are attached. Richards studied the influence of temperature on the rate of multiplication of yeast, when the growth of the population has just begun and this influence is uncomplicated by the inhibitory action of the excretion products. He found that the rate of multiplication of yeast increases regularly with increase of temperature between 4° and 30°. Above 30° a decrease in the rate of growth is associated with an increase in temperature.

In order to study the influence of temperature on the density of saturating population of the yeast *Saccharomyces cerevisiae* several series of experiments were made by the present author. The stock 12, originated at the Berliner Gärungsinstitut, was used. The nutritive medium was the so-called yeast fluid, prepared in the following way:

20 gr. of dry pressed beer yeast were diluted in 1 litre of distilled water, then boiled during half an hour in Koch's boiler and filtered through infusorial earth. To this mixture 5 per cent of sugar was added and the medium was sterilized in an autoclave. The sterile medium was aseptically poured into the test tubes, which had been first sterilized by dry heat. The inoculation was made by means of a sterilized pipette, two drops of yeast mixture taken from a culture of a 30 hours growth at a temperature of 28° being introduced into each tube. All the experiments were made with tubes of about 13 mm. diameter, and 10 cc. of nutritive medium was poured into every one of the tubes. All possible precautions were taken to standardize the conditions of experimentation and to prevent any infection of the medium.

The test tube filled with nutritive medium and closed by the cotton wool stopper, all of them sterilized, constituted the microcosm in which the growth of the yeast population took place. A certain number of hours after inoculation the size of the population was measured. The number of cells in a unit of volume was not counted, but the entire mass of yeast was determined by centrifugation. This method seems to be very accurate and permits many determinations to be made in a short time. Because of the difficulties in obtaining successive determinations on the same yeast culture, the method of observing the progress of growth was to measure groups of cultures at different ages and form an average measurement at each age. The description of the growth of yeast is given in terms of the progress of these averages from one age to the next. It has been shown by Merrell (23) that the form of the growth of these averages can not be assumed to be characteristic for the growth of the separate cultures. Separate curves may differ in certain fundamental characteristics from the general curve.

In the curves reproduced here each point corresponds to the measurement of yeast in six tubes at the same time. Altogether three series of experiments embrace 451 measurements. The centrifugation was carried out in the following manner:

the contents of a test tube with yeast were centrifuged during one minute in a special tube, placed in an electric centrifugal apparatus making 4500 revolutions per minute. After this the liquid was poured off and the yeast cells sedimented on the bottom were shaken up with a small quantity of the remaining liquid. The mixture thus obtained was transferred by means of a pipette into a short graduated glass tube, of 3.5 mm. diameter. This mixture in the graduated tube underwent a second centrifugation during 1.5 minute and then the volume of the sediment was rapidly measured with the aid of a magnifying glass. This method proved to be very satisfactory.

Table 5 gives the chief data on the influence of temperature on the growth of yeast. The conditions of the experiments in each of the series were the same and we

TABLE 5

The influence of temperature on the growth of the yeast Saccharomyces cerevisiae

FIRST SERIES

5.7°		15.0°		28.0°		39.0°	
Days	Amount of yeast	Hours	Amount of yeast	Hours	Amount of yeast	Hours	Amount of yeast
5.5	0.70	22.0	0.90	8.0	0.80	8.0	0.90
9.5	1.49	37.0	2.90	13.5	2.95	13.5	2.50
13.5	2.43	59.0	4.60	17.5	3.50	17.5	2.23
18.5	2.71	72.0	7.30	24.5	7.50	21.5	3.07
21.5	3.16	84.5	6.90	30.5	9.50	24.5	2.43
26.5	3.02	95.0	10.00	37.0	9.10	30.5	3.10
31.5	3.23	110.5	8.75	42.0	11.30	37.0	3.17
35.5	3.28	116.5	7.85	59.0	10.90		
		135.0	8.30	66.0	10.70		
		156.0	8.40				

SECOND SERIES

5.7°		15.0°		28.0°		39.0°	
Days	Amount of yeast	Hours	Amount of yeast	Hours	Amount of yeast	Hours	Amount of yeast
4.0	0.23	16.0	0.12	6.0	0.18	4.0	0.18
8.0	0.50	32.0	1.00	12.5	1.28	8.0	0.65
13.0	1.82	48.5	2.82	18.0	3.20	12.5	1.44
16.0	2.09	75.5	5.63	24.0	5.22	16.0	1.68
21 5	3.05	96.5	6.43	30.5	7.28	20.0	1.84
26.5	2.43	119.0	7.27	36.0	9.08	36.0	2.02
30.5	2.50	144.5	8.14	42.0	8.78	40.0	1.95
		168.5	7.32	48.5	8.73		
				73.5	8.45		

THIRD SERIES

28.0°		33.0°		37.0°		41.0°	
Hours	Amount of yeast	Hours	Amount of yeast	Hours	Amount of yeast	Hours	Amount of yeast
6.0	0.16	4.0	0.12	4.0	0.18	3.0	0.06
13.0	1.60	9.5	1.56	9.5	2.00	6.0	0.18
18.5	3.17	13.5	3.12	13.5	3.40	9.5	0.24
24.5	5.87	18.0	4.93	18.0	4.57	13.5	0.36
31.0	6.30	24.5	5.80	24.5	4.82	18.0	0.58
38.5	8.77	31.0	7.87	31.0	4.82	24.5	0.48
44.5	9.63	38.5	6.30	38.5	4.30	31.0	0.24
50.5	9.28	44.5	5.83	44.5	4.66	38.5	0.26
61.5	9.74	50.5	6.95	50.5	4.11		
73.5	8.93	61.5	7.27				

can compare directly the growth of yeast in different temperatures within the same series. However, different series cannot be compared directly with each other, as the nutritive medium was not prepared at the same time and therefore slight differ-

ences in its composition might have occurred. The examination of table 5 makes it evident that temperature has a pronounced influence on the rate of growth of the yeast population. For instance, the population attains its asymptotic value at a temperature of 39° twenty-eight hours after the beginning of the experiment, and in a temperature of 5.7° only after twenty-

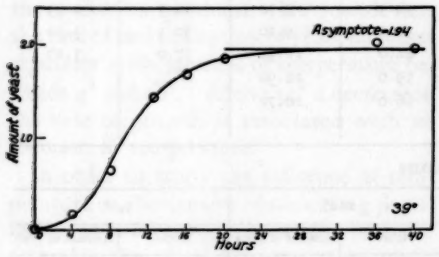

FIG. 13. THE GROWTH OF THE YEAST SACCHAROMYCES CEREVISIAE AT A TEMPERATURE OF 39° (SECOND SERIES)

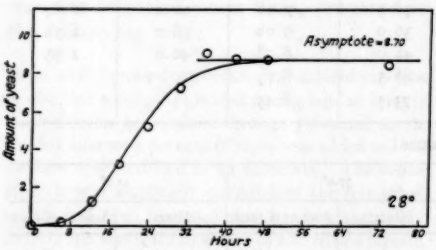

FIG. 14. THE GROWTH OF THE YEAST SACCHAROMYCES CEREVISIAE AT A TEMPERATURE OF 28°. (SECOND SERIES)

eight days. Figures 13, 14 and 15 present the curves of the growth of yeast at different temperatures according to the second series of experiments. The analysis of these curves shows that we have before us skew logistic curves. We fitted the equations of these curves given in table 6.

Inserting in the place of x the number of hours passed from the beginning of the experiment we obtain the quantity of yeast in divisions of our graduated tube (y). The curves in figures 13, 14, and 15 have been plotted according to these equations.

Let us consider now the relations between the asymptotic population and temperature. The levels of the asymptotic populations in different temperatures have

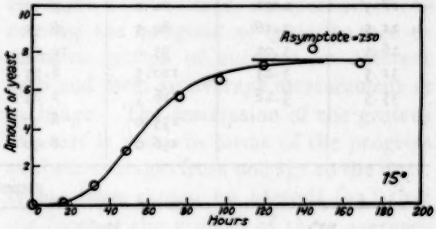

FIG. 15. THE GROWTH OF THE YEAST SACCHAROMYCES CEREVISIAE AT A TEMPERATURE OF 15°. (SECOND SERIES)

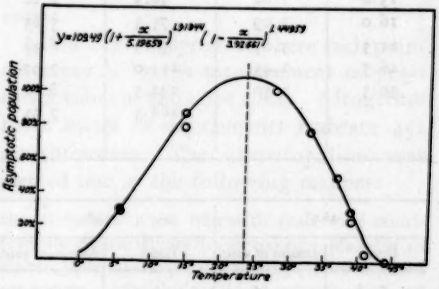

FIG. 16. CONNECTION BETWEEN THE LEVEL OF SATURATING POPULATION AND TEMPERATURE IN THE YEAST SACCHAROMYCES CEREVISIAE EXPRESSED WITH THE AID OF THE PEARSON CURVE, TYPE I

been established on the basis of the data of table 5. These values are presented in table 7. In order to make the comparison of different series possible we have used the following procedure: the level of asymptotic population at 28° was taken as 100, those at other temperatures were expressed in percents. Figure 16 represents these data graphically. It shows clearly

that temperature has an influence on the density of saturating population. The population density decreases with a deviation of the temperature from the optimum whether it falls or whether it rises. The influence of a rise of temperature is sharper and the right side of the curve is somewhat more steep. Therefore our curve has a negative asymmetry. For the mathematical expression of the relation between population density and temperature we have used a Pearson curve of Type 1. Figure 16 gives the equation found and the curve based on it. The Pearson curve gives us a good mathematical description of the relationship under consideration.

TABLE 6

The logistic curves for the growth of the yeast Saccharomyces cerevisiae in different temperatures (second series)

TEMPERATURE	EQUATION OF LOGISTIC CURVE
15°	$y = \frac{7.50}{1 + e^{6.60813 - 0.18127x + 0.001312x^2 - 0.0000038x^3}}$
28°	$y = \frac{8.70}{1 + e^{6.71205 - 0.51168x + 0.01098x^2 - 0.000112x^3}}$
39°	$y = \frac{1.94}{1 + e^{5.17961 - 0.75980x + 0.02610x^2 - 0.000412x^3}}$

TABLE 7

The influence of temperature on the asymptotic population of the yeast Saccharomyces cerevisiae

FIRST SERIES			SECOND SERIES			THIRD SERIES		
Temperature	Asymptotic population		Temperature	Asymptotic population		Temperature	Asymptotic population	
	Absolute	In per cent		Absolute	In per cent		Absolute	In per cent
5.7°	3.20	29.09	5.7°	2.55	29.31	28°	9.30	100.00
15°	8.60	78.18	15°	7.50	86.21	33°	7.10	76.34
28°	11.00	100.00	28°	8.70	100.00	37°	4.60	49.46
39°	3.10	28.18	39°	1.94	22.30	41°	0.425	4.57

DISCUSSION

We can now analyze some of the results of the experimental population study. We have examined the influence of temperature on the density of saturating population in *Drosophila*, in the water-flea *Moina*, and in the yeast *Saccharomyces*. For these three organisms the conditions of experimentation have been different. In *Saccharomyces* we studied the growth of the mass of yeast. It must be borne in mind that the size of the yeast cell is not the same at different temperatures and that the yeast mass at different temperatures does not express exactly the number of cells in those conditions. It is only approximately that the mass can be considered as an equivalent of the size of the population. The cessation of the population growth in yeast and the attainment of an equilibrium depended apparently not on a lack of food but on the accumulation of toxic substances in the medium.

With the water-flea *Moina* not the mass but the number of individuals has been

counted. The quantity of food was kept at a certain level, fresh food water being given daily. Terao says (38, p. 551): "It may be mentioned that the food material was abundant enough for the water-fleas, inasmuch as we found some, even at the culmination of the population growth, left unconsumed at the census time."

In these experiments there was one point common to both the organisms studied: the equilibrium was not due to any deficiency of food. Under such conditions the influence of temperature on the density of saturating population in *Moina* can be expressed by the Gauss curve and in *Saccharomyces* by a Pearson curve of the first type.

The experiments with *Drosophila melanogaster* have certain peculiarities. The entire population has not been counted but only the imago. We do not know the number of larvae nor that of pupae. The food supply was not maintained at a certain level, but twice in the course of the experiment some fresh food was added. This circumstance complicates the analysis of the experiment. We can only remark that the sharp decrease of the density of saturating population at 30° temperature was not connected with any lack of food, as this temperature is close to the optimum for the development of yeast, which is the main food of *Drosophila*.

Hence it is evident that the temperature has an influence on the density of saturating population, and the generalized curve of Pearson can be used to express this influence in mathematical terms. Future investigations must elucidate what are the causes of this type of relation by a detailed analysis of the population growth of different organisms.

The ecology of populations is one of the branches of physical biology (Lotka, 21), which studies organic systems with the aid of physical principles. The influence of the environmental factors on the growth and equilibrium of these systems has been up to the present but little investigated. At the same time the study of these questions is of great importance both theoretically and practically. Chapman (7, 8) is perfectly justified in pointing out that the quantitative study of the influence of ecological factors on insect populations is absolutely necessary. It will enable us to predict the size of the population in the conditions of nature, which is very important from the point of view of an economic entomologist.

In the domain of theoretical agriculture Mitscherlich (20) has recently proposed a mathematical expression of the influence of several factors on the yield. We can consider the yield as an increase of organic matter in a unit of time—one generation. This distinguishes it from the quantity of organic matter saturating the microcosm, which we have been considering in the present paper. The problem of the connection between the size of the yield and several environmental factors, successfully solved by Mitscherlich, belongs to the same domain of physical biology.

By studying the influence of ecological factors on organic systems we shall be able to recognise the laws governing the structure of the biosphere, this peculiar envelope of our planet saturated with life. Lately the well-known Russian geochemist V. I. Vernadsky (41) has pointed out the importance and the need of its thorough investigation. The biosphere consists of films and condensations of living beings and is characterized by a complicated structure. The study of the dependence of the density of the films of homogenous living matter on ecological factors, which has been the subject of this paper, is one of the ways of extending our

knowledge of the distribution of the organic matter in the biosphere.

SUMMARY

The field and experimental study of the influence of different ecological factors on the density of population has allowed us to draw the following conclusions:

1. The correlation between the density of population of very different organisms and ecological factors in natural conditions can be expressed by means of a special type of curve, that of Gauss generalized by Pearson.

2. This enables us to take the mean value and the standard deviation for an exact characterization of the average contions and the ecological plasticity of a species. It has been found that there exists a close connection between the ecological plasticity of a species and the position of its average conditions on the ecological scale.

3. The experimental study of the influence of temperature on the density of saturating population of different organisms has shown that temperature influences the density of saturating population. In the two cases studied this influence can be expressed mathematically by means of the Gauss curve in one case and Pearson's first type in the other.

4. It remains for future investigations to discover, by an analysis of the population growth of various organisms, to what causes this type of connection is due.

The author is deeply indebted to Dr. W. W. Alpatov and Dr. Eugen Smirnov for many valuable suggestions and interest in the present investigation.

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SOME DEVELOPMENTAL RISKS THE DORSAL MID-LINE

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INHERENT in all development is a certain element of risk, there is always the chance that the varied and complicated processes involved may be more or less seriously compromised or even thwarted entirely. The fertilized egg, with all its intricate and far-reaching capacities, carries no guarantee that these potentialities will ever materialize, no real assurance that the proper and normal results of development will be achieved. This uncertainty, this possibility of going wrong, is ingrained in the very nature of life. Development is, in all cases, whether it be normal or abnormal, a procession of events which records the interplay of internal and external factors. On the one hand there is the character or quality of the fertilized egg, or of the antecedent germ cells; germinal, hereditary agencies which are part and parcel of living matter itself. On the other hand is the vast and varied environment in which life is immersed; the conditions out of which it came into being, and to which it must ever adapt itself.

Neither of these developmental factors is, in the very nature of the case, constant and invariable and only if both are normal and favorably disposed can proper results be expected. Either set of factors alone, moreover, if they deviate too far from some mean status, and the limits here may be rather narrow, can easily alter and disrupt development or even arrest it completely. The more one factor, or set of factors, departs from normal, mean conditions, the greater becomes the necessity that the remaining influences should be especially favorable. The internal, or germinal, factors are of particular importance since they prescribe and carry through the normal processes of growth and differentiation, as they also set the limits to which maladjustment and maldevelopment may go, and determine the varying forms and characters which such abnormal development may assume. Although the surroundings in which life may find itself, either as single cells or as complex organisms, may either make or mar the future, or finished individual, still this environment does little more than provide the opportunities, more or less favorable or adverse, for some particular bit of living matter to express itself.

That this expression is not always the same, even in forms which have a common origin; and that it is not always successful, even in the face of what appear to be the same surroundings, is as much the rule as it is the exception. One of nature's provisions against this inevitable uncertainty or loss is the almost limitless wealth of animate forms in their incipient stages. If nature cannot guarantee a continuance of life, she can at least make it highly probable by sheer weight of numbers, by a multitude of forms, none perhaps strictly identical, but among which there will surely be some good seed, and that good seed may fall upon good ground. To continue the teleological figure, nature's chief concern here is the environment, with all of its natural perils for future development. If she can do

relatively little to avoid or to combat these dangers and accidents, she can, on the other hand, offset the probable losses by a greater initial expenditure. In this profusion, really an excess of life, there are a number of material advantages. Not only are the chances that any given forms will be preserved very much increased, but the possibilities for variation are likewise enhanced; opportunities, or demands, for newer or more perfect adjustments and adaptations make their appearance, and so the material is provided upon which various kinds of selection can exert their influence.

GERMINAL STABILITY AND VARIABILITY

In contrast with the vagaries and uncertainties of the environment, which, in their effects upon development, may range all the way from an ideal setting to the most impossible conditions, there stands the relative constancy and stability of the internal factors, the germinal organization. This organization, which is the beginning, and, in a way, the end of life, the ultimate source of all its activities and manifestations, is itself, however, not immutable, not exempt from the influences which play upon living material in general, but, like that material, of which it is a part, it is subject to change and gradual transformation. Although undoubtedly the stability of these germinal, or hereditary factors, is their chief and most important characteristic, that stability is relative only and not absolute. Its primary function is obviously to preserve, as it were, the *status quo*, to maintain and continue the ancestral line in all of its essential features, but that stability is not of such a degree or of such a character as to preclude the possibility of gradual and eventually profound alterations when sufficient provocation or suitable opportunities present themselves. The whole history of life upon the earth, and of every individual creature, is but the story of the stability, or stubbornness, of hereditary influences on the one hand, and of their variability and plasticity on the other.

It is with certain aspects of this germinal variability and stability and of their significance in development that we are especially concerned at present. As this apparently contradictory combination of characters, a sort of unstable equilibrium, is the starting point and basis for all future development, so it is, in turn, the product of all previous development. Behind each and every individual is an interminable and unbroken ancestral line; back of the germ plasm lies a phyletic history of equal length, parallel and comparable throughout. The stepping stones in phyletic history are furnished by the modifications which have been brought about in the germ plasm. Its variability and plasticity, if we may be allowed to continue the figure, have made it possible that there should be steps, either up or down, rather than a dead level of continual sameness; its stability and constancy have enabled it to support the ever-increasing load upon it. How modifications in germinal factors may have been accomplished, need not trouble us at present, their existence and variability are of more importance.

If there is a phylogeny and an ontogeny of the individual and of the tissues and organs which compose him, then it is equally true, and for the same reasons, that there is a phylogeny and an ontogeny of the germ-plasm of the germinal factors which underlie and are responsible for all development. As there are in any organism characters of varying phylogenetic age, so there are hereditary factors of varying age and significance. As we recognize bodily features which are constant or

variable, so we find among the germinal influences those which are always present and operative, as well as others which may be absent or effective only under certain conditions. As different parts or characters of the organism may exhibit a varying susceptibility or a disposition to react in different ways to various influences, so also do hereditary factors show a differential susceptibility, some are more easily affected than others and the end results of their activity are not always the same. This separation and contrast between the hereditary make up and the finished product is naturally artificial and unreal, since the latter is simply the outgrowth of the former, a sort of incarnation; but the comparison may be of service in indicating that what is ordinarily predicated of the individual, his present condition as well as his past history, his general character and structure as well as his own peculiarities, is, in large measure, also true of the germinal elements from which he arose. As any given organism may be looked upon as the last representative of a long phyletic line, the product of innumerable generations, so, likewise, his own germinal elements are the last of a parallel and comparable series. The capacities and qualities of the latter, like the present condition and characteristics of the former, have been slowly and gradually built by countless modifications of various kinds; accretions on the one hand with losses on the other, new features have arisen and older ones have dropped out, advances at one point with recessions at another, periods of quiescence have alternated with slow or sudden changes, a curious mixture of old and new, of constant and inconstant, of important and unimportant. The germ-plasm, like the finished form, must be seen in its proper perspective, and of course this is true of the organism at any stage of its development. There is a background of great antiquity and of relatively great stability against which are seen, or out of which emerge progressively, a host of minor, variable or even latent features, newer or older, and of greater or less importance. To be sure, life in any form, or at any stage, cannot be separated or considered apart from its environment, but that environment can hardly bring about any thing that is not already, in some way, implicit in the material upon which it works.

In the majority of cases development may be expected to pursue its accustomed course, at least as regards its essential features, but the very complexity, sensitiveness, and variability of its germinal basis opens wide the door to all manner of aberration and derangement. The mechanisms which preside over orderly and proper development are, in large measure, the same as those which allow abnormal development and determine its particular character. Ordinarily of course, the former influences are in the ascendancy, they are possessed of sufficient vitality and momentum to achieve their purpose, but there are always lurking in the fringes, latent, weaker, often unfavorable possibilities, which may only await the opportunity to manifest themselves, and this opportunity is often furnished by environmental disturbances. One might speak of these factors as dominant and recessive, but here these terms have a much broader and more general significance than is usually attached to them. This dominance may be, and often is, of such a degree that its effects can hardly be entirely suppressed, however much they may be distorted and unrecognizable, while the recessiveness of certain characters may be so complete that only very exceptional circumstances ever reveal their presence.

It is well known that abnormal development is more frequently seen in certain parts of the body than in others, that it has a tendency to conform, more or less closely, to certain types or even that certain types predominate in certain animals. That these disturbances are brought about relatively early, as a rule, is the natural consequence of the early formation of the structures involved, but behind this is the fact that at this early date these structures possess a far greater and more complicated potentiality for development, either normal or abnormal, than they do at any subsequent stage. Parallel with the progressive differentiation of tissues in general there is a progressive and inevitable decrease and simplification of their original capacities, and the farther development proceeds the less likely is it to be deranged and such disturbances as may arise are less extensive and less radical. All of this points to the great importance of internal factors in aberrant development, regardless of the rôle which external influences may play in preparing the ground for it, and that rôle is certainly no small one. It would appear as if the more nature has packed into cells, in the way of capacities and potentialities, the greater becomes the risk, in the subsequent unpacking, that the final results will be not only dissimilar, but even inadequate or quite unfitted for their intended purposes. To what extent this may have some special application to human ontogeny will appear later.

THE DORSAL MID-LINE

Of the parts of the body, and more particularly of the human body, which are not infrequently disturbed in their development we need only mention the extremities, especially their distal portions, the general region of the head and face, and the mid-line of the back. It is with the last of these only, the dorsal mid-line, that we are concerned at present. Conditions here seem rather more simple, the evidences for certain underlying influences in maldevelopment are clearer than elsewhere, and it is also easier to bring forward suitable material by way of illustration.

One of the earliest and most momentous of embryological processes is that which prepares for, and initiates the development of the central nervous system. This occurs in a part of the embryonic body, in the blastoderm, which has already been, or still may be, the seat of very profound and significant changes, the general region of the blastopore. The fundamental alterations which have been going on here, in the axis of the blastoderm, antedating for the most part, the formation of the nervous system, are of a most extreme antiquity and of the very greatest importance for all future development. They do not, however, concern us particularly at present, beyond their obvious relation to the general integrity and proper quality of the structures which they may influence. They are of interest here for theoretical rather than for practical reasons, the possibilities are doubtless very great but very little might be demonstrable. In what follows we shall have little occasion to go behind the development of the nervous system. This does not mean, of course, that our problem begins here, and not earlier, but simply that the field for discussion has been simplified or restricted to that extent.

In the formation of the vertebrate nervous system and some related structures, certain conditions prevail which are absent or much less in evidence in development elsewhere. The general tendency of these conditions is to contribute to or accentuate the variability and in-

stability of the structures in question; because of their presence, the nominal risks of development are increased, and perfect, or even average, results are rendered just a little less certain.

Some of these compromising influences or conditions can be traced to the general character and function of the epithelium which covers the animal body. Few, if any, structures can boast a more venerable antiquity than the external covering of living forms, and certainly none have had to meet such varied and important demands or have responded to them with such a profusion of derivative features. This body covering, or envelope, has always played a dual and well-nigh paradoxical rôle, where almost contradictory characters would seem called for. On the one hand it has shut in, or enclosed, so to speak, the animal within itself, while on the other it has been called upon to mediate between the animal and everything without. It has been at one and the same time, a barrier, practically complete and insurmountable between the organism and its environment, as well as a wide open means of communication between that organism and that same environment; skin and derivatives in one rôle, nervous system and sense organs in the other. All of these conflicting characters must be packed away, in some form, in the germ cells and in the fertilized egg. At the proper time and in response to proper stimuli they must again be unpacked, gradually sifted and suitably allocated in the surface cells of the developing embryo. Complicated as conditions already are, they must become even more involved as newer features make their appearance in phylogeny, and as newer capacities and tendencies are superimposed upon, or become incorporated in, older and more fundamental hereditary factors. From some primordial or potential ectoderm, primitive skin, there are to be derived, in principle, not only skin and nervous system, but also the much younger and often very precocious and extensive epithelial coverings of the embryonic membranes, chorion and amnion. These phyletic innovations must find their proper place in ontogeny: they appear as cenogenetic characters, whose extensive and often extremely precocious development, the new and highly important function which they must subserve, the fact that the factors which control them are not only relatively new but must become operative long before the time which their phyletic rank might indicate, and finally the paramount rôle they play in relating the organism to its embryonic environment, all conspire to throw an added burden upon internal developmental factors and render deviations in that development, whether slight or serious, a little more probable. The preparation of a chorionic or trophoblastic shell, along with its associated connective tissue and vessels, and the formation of an amniomedullary cavity, as it is carried out in various ways in amniotes, is a very different thing from the relatively simple requirements of the ectoderm in anamniotes. These newer and increased requirements, and secondary complications, may well stand in some relation to the disturbances and maladjustments which are not infrequent in the earliest stages of amniote development; altered nutritional conditions among others, various aspects of what has been called faulty implantations and many of the variations or even grosser changes which are so common in the embryonic membranes in man. One is reminded of the great variability of the chorionic vesicle, of its size and thickness, the numbers and character of its covering villi, and of the peculiarities exhibited by the contained magma. Even the

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relatively simple amnion is subject to no little variation, the possible consequences of which have been recently alluded to by Streeter (1931). Here may be found some of the influences, which, in conjunction with unfavorable surroundings, take such a heavy toll of human life during the early weeks of intrauterine development.

After the formation of the epithelial coverings of chorion and amnion, there remains the embryonic ectoderm proper, at this stage more comparable with the ectoderm of anamnia, but still differing from, or surpassing, it in its peculiar hereditary qualities; qualities which differ from one form to another and which, in man, reach their highest capacity for the formation of nervous system, while as regards skin and derivatives these capacities may be rather restricted.

THE VULNERABILITY OF THE DORSAL MID-LINE

In the formation of the nervous system and of what might even be termed a new dorsal mid-line, there are a number of factors which conspire to make this particular part of the embryo unusually susceptible and vulnerable. We have already noted the peculiar qualities of the parent tissue from which arise both nervous system and skin, as well as the newer functions which it has acquired for the protection and nutrition of the embryo. But these complicated endowments must be subjected in their turn to relatively gross and massive morphological alterations in the arrangements of cells, and these spatial shiftings and readjustments always constitute a very definite risk in development. In the formation of the medullary folds and their subsequent inrolling and fusion to form the neural tube not only are there involved very large masses of tissue, but that tissue is by nature especially sensitive and vulnerable. The very character of the embryological processes, and of the material with which these processes are carried out, makes development in this region unusually precarious and uncertain.

Hand in hand with the development of the neural tube there must be the proper restoration of continuity in the superficial layers over it. If the neural tube fails to close and retains its connection with the surface cells, the consequences for the normal development of the structure which should cover it over are obvious and inevitable. But conditions are not always as simple as this, and the proper closure and separation of the nervous system does not guarantee the integrity of the parts dorsal to it. Everything indicates that there has been impressed upon the dorsal mid-line, from the nervous system out to and including the skin, a lability and vulnerability, which can hardly be matched elsewhere in the body. As far as the nervous system is concerned, particularly in regard to its grosser defects, conditions are quite intelligible; but it is not so easy to find equally tangible reasons for those minor derangements which leave the nervous system quite untouched and which manifest themselves only in the younger and more superficial structures. It would appear as if the whole dorsal region had been in a measure unsettled by the events which take place here and by the peculiar susceptibilities of the tissues involved. Whatever the predisposing or exciting causes may be, their effects are regional rather than structural; any or all parts in the mid-line may be affected, more or less alone or in various combinations.

Although the ventral and dorsal limits of what we are calling, at present, the dorsal mid-line are always definite and concrete, as nervous system and integument, the lateral boundaries of this axial

region are not only indefinite but also subject to considerable variation. In view of the embryological conditions and of the influences which may be at work here, the former limits are natural and simple, but there is little or nothing to indicate where one might expect to find the lateral limits. Actually the vulnerable region of the back appears as a region of considerable width, often much more extensive than the nervous system beneath. Either the abnormal influences which may be in evidence here, and which are especially concentrated in the axis of the body, are also effective at some distance from the mid-line and involve cells which are potentially if not yet actually a part of this dorsal region, or the tissues which later find their way into this area become secondarily affected with the common taint. Of these possibilities the former would appear the more reasonable, although, naturally, any initial axial defect may easily entail secondary and wide spread deficiencies at later stages.

It does not seem possible to escape the conclusion that there is inherent in the dorsum of the body a peculiar sensitivity, variability, and even vulnerability which may manifest themselves in a great variety of ways. This condition would appear to be the natural and inevitable result of the materials and processes involved; materials which are, in the nature of the case, sensitive and charged with varied and far-reaching potentialities, processes which are radical and extensive and fraught with wide-spread consequences. The frequency and variety of dorsal anomalies have their ultimate source in the innate qualities of the constituent cells and the peculiar growth processes to which they are subject.

Without attempting, in any particular case, to determine the relative importance of internal or external factors in maldevelopment, certain alternatives may be noted. Taking the future or potential organism, at any stage of the life cycle, as gamete, zygote or embryo, and assuming a normal or average quality or capacity, one would expect that unfavorable external influences would pick out the weaker and more vulnerable characters as presented at any particular stage. The point of attack may be masses of cells, individual cells or simply certain specific qualities or factors in some of the cells. These weak points are furnished, to a large extent, by the germinal composition, varying from individual to individual, and by the peculiarities of various developmental processes. But this "weakness" is essentially a relative one, and if the environmental disturbances be sufficiently severe or of a certain quality, other much more stable factors and growth processes may ultimately break down and a general disorganization or arrest of development may result. Among the weaker, more vulnerable factors are those which are responsible for the formation of nervous system and of the structures dorsal to it. But this natural or normal susceptibility may be accentuated and appear as an hereditary taint, until finally normal development may be the exception rather than the rule. Hereditary defects have a very definite tendency to pick out parts of the body which are inherently susceptible to various influences, notably extremities and head. These apparently occur with little or no reference to external influences; rather than a weakness which allows of, or predisposes to, derangement, there is here a positive bent in that direction and the normal growth processes are or may be, overruled. Somewhere between these and average conditions one might seek the genesis of hereditary malformations. Somehow the relatively unstable germinal

or internal factors involved may have been disturbed or upset, modified perhaps, and these new conditions, though variable, may become quite as stable as those which they supplanted. This would appear to be very similar if not essentially the same as the mutations of the geneticist, but there is no necessity that the heritable defects be identical, nor that they conform strictly to mendelian principles. Environmental influences might still very well be a factor in determining whether or not such defects might appear as dominant or recessive.

It would not seem as if there were any great and impassable gulf fixed between hereditary and many other types of maldevelopment. Internal factors are effective and essential in both; in the former they are more constant and conspicuous and the end results show less diversity, while in the latter the effects are more erratic, often more extensive and the rôle of the environment is more often in evidence. In as far as both show a special predilection for certain parts or constituents of the body, they indicate a special susceptibility and instability of these parts, and these characteristics are essentially germinal and hereditary. This does not mean that the environment may not play an important part in the genesis of mal-formation nor that it might not be of some significance even in the case of hereditary anomalies. The weak points in the chain of developmental events may be, and in the great majority of cases are, strong enough to maintain themselves under normal or average environmental conditions, provided that the hereditary make up is of equal quality; but they are nevertheless, the points at which development is most certain to give way if the surrounding conditions become unfavorable, and this danger is even more enhanced as internal factors themselves become weaker, more variable or more defective. In the egg or embryo, as in the adult, it may be external influences which provide the opportunity for otherwise inactive or latent hereditary capacities or propensities to manifest themselves. It is in the mid-line of the back that conditions are especially conducive to all sorts of aberrant development and the blame for this must attach largely to internal factors, although external influences may often be required to bring about these results.

In considering the dorsal mid-line as a developmental risk, we have been interested in the underlying factors which contribute so largely to that risk, rather than in the final results of maldevelopment here. The almost endless variety of anomalous conditions which may be encountered on the dorsum is too well known to call for any repetition at this time. There may be involvement of part or all of the central nervous system, the overlying structures; bone, skin, etc., may be more or less conspicuously affected, various combinations of anomalous features may occur or varying grades of the same condition, while in importance the range is all the way from the slightest variation to gross deficiencies quite incompatible with independent existence. It is not always a question of a defect as such, a too little of anything, for there may be excesses, as there may also be structures or tissues more or less foreign to this region. Indeed it is the great diversity of conditions here which is of special interest in indicating the importance of internal factors in development.

Among the minor disturbances in this region we need mention only those exhibited by the skeleton, skull and vertebral column, and by the integument. Vertebral anomalies and defects are especially common, they involve as a rule

only the dorsal part of the vertebra and are most frequent in the mid-line or symmetrically disposed on either side. The derangement in the skeleton, however, may be more extensive and in severe cases there are often associated anomalies in the vertebral ends of the ribs (Hamilton). In the skin there may be anomalies, usually excesses, in the pigmentation, vascular supply or in the development of hair.

In addition to the numerous defects of various kinds which are known chiefly from material at term, or even later, there is a very considerable body of evidence, from the early weeks of intrauterine life, which points quite as unmistakably to a very definite vulnerability of the embryonic dorsum. We refer especially to the extensive observations of Mall (1908, 1917) and Mall and Meyer (1921). Many of their cases as well as much of our own material from the first two months of development assumes an especial significance in the present connection. Although the majority of these specimens are pathological, sick embryos rather than simply young terata, more probably the victims of an unfavorable environment than of any hereditary shortcomings, they nevertheless show their peculiar and often characteristic changes most frequently somewhere along the dorsal mid-line. While in some instances there may be frankly teratological conditions which have suffered secondarily along with the rest of the embryonic body, there are a very considerable number of cases where there seems to have been no previous malformation at all, and where everything points to pathology rather than to teratology. Here belong a great variety of conditions: more or less extensive losses of the superficial ectoderm, abnormal thickening and pigmentation, superficial or deeper blebs and vesicles, and the blisters and ulcerations which Mall noted so often. These local disturbances or alterations in the tissues are often quite slight and superficial although they may extend deeply enough to involve the nervous system. One gets the impression that they are the results of some damage, possibly chemical or nutritional, to average, previously healthy tissues; many of them seem to have been of relatively short duration and in others it would seem as if healing and restitution might still be possible. The fact that in practically all of these cases there are more or less extensive and characteristic alterations in the membranes, and that the embryos themselves give ample evidence of secondary changes, would indicate that external influences are chiefly if not entirely to blame. These young pathological embryos are especially illuminating as examples of the reactions of a sensitive and vulnerable part of the embryo to an unfavorable environment. They differ from the typical monster or malformation not so much in the tissue or locality involved but rather in the type and character of the reaction brought about. Some of these peculiar reactions, as they are encountered in early human embryos, will be described and illustrated more in detail on another occasion, and a number of similar or related conditions may be found in the works of Mall, and Mall and Meyer, noted above. The possible consequences of some of these slighter defects, in cases where development goes on to term, we shall take up elsewhere.

It has already been suggested that the peculiar conditions which obtain in the dorsal mid-line may have an especial significance for human development, as contrasted with the development of lower, even other primate forms. The significance of these conditions is brought

out by the unusual susceptibility of this region early in development, as witnessed by the great frequency with which it is the seat of disturbed development of one kind or another. Another expression of these same conditions may be found at term, or later in life, in the marked variability of certain dorsal structures. This increased vulnerability and variability is an expression of the increased variability and relative instability of those factors which bring about development; the instability of these is, in turn, the natural result of the newness and the inherent variability of those structures for whose development they are responsible. The internal developmental factors which must bring about the proper and adequate formation of the human nervous system and of the structures which cover it over and protect it, have not simply the nominal task, and risk, of amniote or even primate development, but the added burden of caring for a number of much newer and more variable features, characters which are preëminently human and not yet stabilized. It is this added burden, these later complications and innovations, which make the dorsal region so susceptible in human beings. This susceptibility, though real, may give little or only occasional evidence of its presence so long as environmental conditions remain favorable and essentially normal. But the external factors in human development are not always ideal, or even of tolerable character, perhaps less so now than ever before. These external factors assume a very great practical importance, however, in furnishing the opportunities for maldevelopment, in setting the limits to which internal factors can unfold themselves properly, in determining the extent to which normal influences may be forced into unnatural forms, or in allowing latent, even undesirable influences to manifest themselves.

VULNERABILITY OF THE HEAD

We shall mention only two localities where peculiarly human conditions prevail, and where there appears to be an unusual vulnerability or, more often in milder cases, simply a greater tendency to variation. These are the head and the lumbo-sacral region; the former involved in the great cerebral development of man, the latter concerned, along with some other parts, in the assumption and maintenance of the erect posture. In both cases we are dealing with some of the most recent and least stable attainments of the human family, and in both cases, also, the effects are felt beyond the structures which would seem to be primarily concerned.

In the head the dominating influence is the brain, especially in the earlier stages, and it is this part of the embryo which suffers most frequently and most severely. But the agencies which are at work here are not confined to the nervous system; they affect also the parts which close this in, especially over the dorsum, while the face and more ventral structure are less intimately involved. Naturally there is a very close relation between the character and development of the brain and the structures which enclose it, whether soft or bony. In a sense the primary influences emanate from the brain, and as this enlarges and acquires new characters, corresponding adjustments must be made in the covering skull and scalp. Hand in hand with the development of those hereditary factors which are responsible for the human brain, there must be developed parallel and associated factors to care for the proper covering and protection of the brain. One of the results is that both sets of factors are unstable and vulnerable and the various growth processes over

which they preside become especially prone to injury or disturbance. Theoretically one might attach rather more importance to the influences which bring about the development of the nervous system, or give them a certain degree of priority or dominance, so that as the brain becomes a little more susceptible to derangements in its development, the enveloping structures are likewise a little more likely to be disturbed. In other words, the various anomalous conditions which may be found in the mid-line and back of the head, have in many cases, we believe, a part of their explanation in the fact that there is a human brain beneath. Among other conditions we would note here simply the great frequency of minor, often superficial defects in the mid-line of the head, defects which tend to be limited to the head and even to the mid-line. Numerous examples of these embryonic anomalies, which show a special predilection for the head and scalp, may be found in the works of Mall, and Mall and Meyer, and in our own article which will appear later. It is also significant that the comparatively rare cutaneous defects are most frequent on the head, and typically in the mid-line, often near the vertex. Although the skull may be involved in varying degree along with the scalp, there are, in the bones themselves, frequent evidences of disturbed development. These are most conspicuous and most varied in the occipital bone, and farther forward around and in front of the lambda; substantially in the same locations in which occur the early embryonic defects.

VULNERABILITY OF THE LUMBO-SACRAL REGION

As regards the lumbo-sacral region conditions are again substantially the same. The nominal risks encountered here, as a part of the dorsal mid-line, have been further complicated and enhanced by the appearance of newer and more variable features. We have in mind here particularly the vertebral column; but even the skin, with its frequent anomalies in pigmentation, in the development of hair, etc., as well as the grosser deficiencies which occur here, offers sufficient evidence for the general instability of this part of the body. The lower lumbar column and sacrum are among the most variable bones of the skeleton; here more than anywhere else, normal conditions or slight variations grade imperceptibly into the grossest defects. This variability is not only a question of gross morphology, but of weight of bones and of their functional integrity as well (Ingalls, 1931).

As we assumed that many anomalies of the head are, in the last analysis, referable to the great development of the human brain; so we suppose that lumbo-sacral anomalies owe, in part, their peculiar frequency to the relatively recent modifications which this region has undergone. In regard to the variability of the lumbo-sacral spine we may quote from our recent article in the *Journal of Anatomy*.

> This variability, regardless of how, or to what extent it may manifest itself in any particular case, is traceable to two important phylogenetic processes. One has already been noted, the progressive shortening of the presacral column, or the gradual ascent of the attachments of the pelvic girdle. The resultant fluctuations would indicate, if one may be allowed the expression, that nature has been and still is, somewhat undecided as to just what to do in any individual case. The other factor, not sharply separated from this, has been the development of the erect posture. This has called for structural and functional adjustments in various parts of the body, but as regards the axial skeleton these adjustments are most in evidence where the lower extremities join the spine, in the pelvic girdle and immediately above it. Separating these two influences, for the sake of clearness, it may be said that upon the earlier, somewhat more morphological lability, there has

been superimposed or engrafted a later rather functional variability; with the result that the lumbosacral spine not only exhibits the most varied and bizarre deviations around some kind of a mode, but that even its proper functional integrity may be compromised if not actually endangered. Hence it arises, in combination with other influences, that in this particular part of the body, minor variations pass with such ease and frequency into the grossest teratological conditions.

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EUTELY OR CELL CONSTANCY IN ITS RELATION TO BODY SIZE

By HARLEY J. VAN CLEAVE

(Contributions from the Zoological Laboratory of the University of Illinois, No. 418)

MOST of the text books in cytology and embryology give the impression that cell size in any given species of animal is pretty definitely limited and consequently postulate that differences in size of organs or of the entire body of necessity must be due to differences in number of component cells. The pioneer studies of Conklin and of Minot are commonly cited in support of this generalization. Against this assumption stands a relatively large body of literature giving detailed evidence that bodies of many of the metazoan species are built upon a specific plan of immutable specifications in the number and arrangement of the somatic cells.

The term cell constancy has been frequently applied to this identity in number of component units in an organism, but in many instances the term nuclear constancy has been used in the interest of exactness since so many metazoan tissues lack cell boundaries. Eric Martini (1909) introduced the term eutely into the literature to designate this concept of constancy in number and arrangement of histological units. Since most of the observations on eutely have been made in the course of morphological studies, they have not come to the attention of embryologists and cytologists, or at least have not found their way into text books and have not been incorporated into the current theories of ontogeny and the cytological basis of evolution.

Blind postulation of uniformitarianism has been one of the worst obstacles to the advance of science. In spite of the fact that in nature the same end may be accomplished by diverse means, the dogmatic statement of a partial truth as the whole truth seems to have been firmly established as a practical solution of the difficulties arising from apparent lack of unity in the presentation of scientific results to elementary students. New discoveries consequently find their way with difficulty into textbooks if they seem to contradict or qualify well established beliefs and theories. In many instances, when fully understood, they add strength to other theories and interpretations and become recognized as alternate rather than contradictory explanations of the operations of nature. The early protagonists of natural selection considered it as the onyl possible method of operation in the evolutionary process, just as many Mendelians could conceive of no law of heredity outside the pale of unit characters and Mendelian ratios. In like manner, body size has come to be thought of by many zoologists as determined by the single set of qualifying factors determining the relative number of somatic cells.

CELL LINEAGE AND CELL CONSTANCY

This point of view is especially hard to understand when the logical consequence of the time honored study of cell lineage is seen in its projection into the field of cell constancy. In the closing decades of the nineteenth century the researches of Wilson, Conklin, Mead,

Treadwell and many others depicted in the history of the developing egg a set of conditions which in many instances finds expression in the mathematically accurate and predictable sequence of cleavage stages. The cleavage planes in eggs with determinate cleavage not only follow a definite plan expressible as laws of cleavage, but the blastomeres resulting from cleavage bear predictable spatial relations one to another and may be traced not only as cell groups but individually through the maze of cleavage products until the rudiments of systems and organs are recognizable. Thus an intimate knowledge of the individuality of the blastomeres grew into the fulfillment of a prophecy as to what particular organs or structures of the adult are to be derived ultimately from each of the cells of early cleavage.

These studies in cell lineage formed a background for a mechanistic interpretation of ontogony which gave incentive to the development of experimental embryology and cytology. Some experimentalists hoped to find in the organization of the undivided egg an explanation of later events leading to a separation or segregation of organ forming substances. It was very natural to assume that since the egg pursues a predetermined course in its development, the power of guidance of the course must be resident within the egg or develop progressively, *pari passu*, with the production of new sets of conditions accompanying the cleavage process. Something closely akin to a conscious, resident direction of development seemed to be demonstrated when isolated blastomeres were discovered to have the power of reorganization so that the separated fragments of a cell group could proceed to develop as independent wholes rather than as fragments. Especially was this true when Morgan, Driesch, and other investigators found that embryos developed from isolated cells of the first cleavage tend to have only half the number of cells present at any given stage when compared with the normal embryos of similar advancement. It would seem that the direction and control of the number of cells is more nearly rigidly predetermined than is the control of the number of persons or individuals which these cells are to form. Individuation, which has usually been considered the goal of the ontogenetic processes, is thus secondary in some embryos to the inherent tendency to attain a goal expressed in terms of relative number of cells.

Few zoologists have appreciated the significance of these findings in the fields of experimental embryology and cell lineage in an interpretation of the organization of the adult individual. If the factors which bring predictable regularity into the cleavage process continue to operate to the close of the embryonic period, the resulting organism would be composed of a number of cells predetermined in the organization of the fertilized egg. In spite of the fact that determinate cleavage finds its logical termination in a fixed number of cells in the adult body, no one has ever transgressed the boundary between logic and science by furnishing an unbroken series of observations on the cellular history of any organism through cleavage to differentiation of the adult cells. Most of the observations on cell constancy have been restricted to those organisms having a relatively small number of cells, for physical limitations of observation and possibility of error in reconstruction are too great to permit proof of either constancy or inconstancy in cell numbers for many large organs. Even in organs of minute size and extremely small number of cells, errors in reconstruction and in interpretation of

sections may completely invalidate observations and conclusions based upon them (see Van Cleave, 1922).

FORMS SHOWING CELL CONSTANCY

To the person unfamiliar with the special literature, eutely or cell constancy may seem an inconsequential phenomenon limited in its application to a very few aberrant groups of organisms. Contrary to this assumption, it has become established in varying degrees in many of the major divisions of the animal kingdom. At the threshold of the vertebrate subphylum, examples of cell constancy have been clearly demonstrated in the Tunicata. Among the arthropods, numerous isolated evidences of constancy are known for the nervous and sensory organs, and particularly among the insects the whole science of chaetotaxy rests upon a precise mechanism for the setting apart of definite numbers of setigerous cells in fixed locations for the production of bristles. Many other examples of at least partial constancy have been demonstrated for insects and their larvae. Researches on annelids produced evidence of constancy in number and arrangement of cells in the larva of Polygordius and in certain cells of the nervous system of other annelids, especially the leeches. The rotifers and Gastrotricha have been favorite examples of absolute constancy. Pioneer studies on the nematodes yielded at first isolated instances of constancy for single organs and later proof of complete constancy for most of the tissues for many forms. The Acanthocephala have varied conditions of constancy but at least in one family every somatic tissue has nuclei of stereotyped number and arrangement. Representing the flatworms, Turbellaria show definite unconfirmed evidences of constancy and among the trematodes gland cells and excretory organs of fixed cell numbers are among the most valued characters used in specific diagnosis, especially of larval stages. Even the epithelial cells of some miracidia are of constant number and arrangement within the limits of the species.

EUTELY AND PHYLOGENY

The forms in which eutely or cell constancy has been demonstrated represent such diverse groups of the animal kingdom that no claim of phylogenetic relationship of these forms may be made. Sinitsin (1931) attempts to show a close relationship between the digenetic trematodes and the rotifers, chiefly because of the common possession of constancy and a fanciful identity in plan of structure. Constancy seems to be the outgrowth of a principle of development from the physiological rhythms which mark most life processes. Such rhythms seem to be coextensive with life but may be suppressed or obscured when numerous additional factors become operative. In the lowest of the Protozoa, standing at the boundary between the plant and the animal worlds, we find the colonial flagellates showing a marked rhythm in nuclear activity which could well furnish the background out of which cell constancy in the Metazoa has stepped. These colonial flagellates with their tendency to form colonies with specific numbers of cells pass on to all metazoan groups the potentiality of a constancy in cell numbers which may find expression in the bodies of the larvae or adults or may be lost because of new sets of conditions entering the developmental program and assuming the rôle of controlling factors.

No student of cell constancy has ever maintained that fixity of cell numbers is universally characteristic of animals. There are many species which we know are built upon a plan permitting of wide

limits in the number of somatic cells. We likewise know that the cells of glandular and some other tissues are often dissipated in their normal functioning. These last named and any organ or tissue which enjoys the powers of regeneration would obviously be excluded from any possible absolute limitation of cell numbers.

Of those organisms which manifest cell constancy, there are two distinct classes: (1) those in which the entire soma conforms to a fixed pattern of cell number and arrangement, and (2) those in which only a limited number of organs or structures have a fixed cellular formula.

CELL CONSTANCY IN HYDATINA SENTA

There have been relatively few forms for which total cell constancy has been demonstrated for the soma. The species for which constancy has been most completely demonstrated is the rotifer *Hydatina senta*. The careful researches of Eric Martini have revealed a total of 958 somatic cells in the female of this species. In order to appreciate the extent of this study a summary of the results is quoted.

The Nuclei of Hydatina senta

I. Skin and associated structures		
subcuticular cells of body and tail	108 nuclei	
foot glands	19	
2 bipolar cells	2	
cingulum	46	
trochus	19	
mouth	43	
between trochus and cingulum	28	
bipolar cells of crown	36	
		301
II. Pharynx		
75 epithelial cells with	91	
38 muscle cells with	42	
nerve cells	22	
ganglion and doubtful cells	12	
	137 cells with	167
III. Digestive tract		
esophagus	15	
stomach	35	
gastric glands	12	
intestine	14	
		76
IV. Urinogenital system		43
V. Musculature		120
VI. Nervous system		247
VII. Retrocerebral organ		4
Total for all somatic tissues		958 nuclei

To some persons, the claim of a cell constancy that makes possible a comparative anatomy whose units are cells and nuclei instead of systems and organs, seems fanciful. Especially is this true when 958 nuclei are crowded into the body of a Hydatina barely visible to the naked eye. But in reality the nuclei are not crowded, in the usually accepted sense of that term, for each nucleus has its own distinctive spatial relations to each of its neighbors and may be compared with the corresponding nucleus of every other individual of the same species.

The writer (Van Cleave, 1922) has reinvestigated certain aspects of the problem of cell constancy in Hydatina with full support of Martini's findings, but with some significant additions to an understanding of factors operating against the maintenance of constancy as brought out later in this paper. A statistical analysis of the degree of conformity was undertaken and for this purpose two structures, the gastric glands and the vitellarium, were chosen because of the ease with which their nuclear contents may be observed. In 435 gastric glands examined, every one showed six nuclei with no tendency to vary from that condition. In 770 vitellaria, 767 held the normal number of eight nuclei, two had ten nuclei and one had twelve. As explained later in this paper these aberrant individuals showed marked evidence of senescence

and in no wise invalidate a claim of absolute constancy in the nuclei of normal individuals of this species any more than would a mutilated specimen.

CELL CONSTANCY IN ACANTHOCEPHALA

In 1914, the writer presented preliminary evidence, which has been expanded more recently, indicating the presence of full constancy in numbers and arrangement of nuclei in Acanthocephala belonging to the family now going under the name of the Neoechinorhynchidae. Four genera are now recognized within this family, all of which have complete constancy in the somatic cells. Even within the same family there may be marked differences in number and arrangement of the nuclei of a given organ or tissue, each characteristic for one or more of the species. The cement gland of the male acanthocephalan shows how a given structure may vary in closely related genera. In the genus Tanaorhamphus, the cement gland contains sixteen nuclei while in Neoechinorhynchus, Octospinifer, and Gracilisentis there are but eight nuclei in the same organ. Thus, in spite of fixity for the species, differences have arisen in the number and arrangement of nuclei within the same family.

As explained in detail in a later section of this paper, most of the Acanthocephala outside the family Neoechinorhynchidae have failed to retain absolute constancy, for some tissues have nuclei that undergo amitotic fragmentation, thereby eliminating these forms from the category of total constancy, though many or most of the somatic nuclei still conform to a perfect pattern of constancy.

PARTIAL CONSTANCY

By far the greatest number of instances of evidence for eutely comprise those cases of partial or incomplete constancy. In these, every quantitative measure of constancy may be found. It was in these forms of partial or incomplete constancy that the principle of eutely was first worked out. Martini (1923: 179) has reviewed the evidence of the early contributions in the studies on nematodes by Looss and Jägerskiold and the more extensive observations and generalizations announced by Goldschmidt. These early workers emphasized the orderliness of arrangement and the regularity in number of the nuclei in the digestive, excretory, and nervous systems of various nematodes. It was left for Eric Martini (1913) to make a monumental contribution in his study on *Oxyuris curvula* which in scope far surpassed any previous contribution to cell constancy in the nematodes. For this species, Martini's monograph establishes constancy in the excretory and nervous systems and in the connective tissue. He found 412 cells constant in all individuals, but the epithelium of the mid-gut, the syncytial epithelium of the body wall, and the genital organs contained a large indefinite number of cells in addition to those for which constancy in number and arrangement could be established.

Martini (1923: 193) has shown that speciation may lead to differentiation of somatic characters without influencing the number of cells. In seven different species of Oxyuris which he studied, all agree in the uniform possession of 65 muscle cells in the body wall. In contrast, a sclerostome from the horse has 87 similar muscle cells in the body wall.

The literature on morphology and histology is replete with instances of organs or structures for which an invariable number of cells has been observed. In many cases these impressions have not

been tested quantitatively and frequently the structures are so large that no absolute proof of either constancy or inconstancy may be applied. The absence of mitotic figures in the central nervous system of all the vertebrates has led to many speculations, one of the most common of which is that there is a fixed number of cells in this system for each individual. Some authors have made comparisons of the number of nuclei in comparable sections of the brain of different individuals of the same species. On the basis of such sampling they have in some instances claimed a degree of conformity that might be considered as evidence of constancy when we consider the elements of uncertainty which enter into the computations.

Certain structures in themselves variable for the individuals of the species are in turn made up of a predetermined number of histological units. The best instance of this condition of constancy within an inconstant structure is the structure of the compound eyes of insects. Each ommatidium is built upon definite specifications with the cells of each not only in fixed numbers but with these units bearing definite spatial, morphological, and physiological interrelations in the functioning of the compound eye. That these ommatida are subject to wide variation has been shown by numerous experiments. Zeleny and his students, working on Drosophila, have found that the number of ommatidia may be greatly influenced by external factors operating at certain periods in embryonic development.

AMITOTIC DIVISION OF NUCLEI

Cell constancy as a block to evolution has been sensed by several investigators. Under conditions imposed by cell constancy, variations which make evolution possible are ordinarily restricted to differences in the form and arrangements of component cells. The only exception to this stereotyped plan of organization would maintain in those instances wherein genes could be affected so that mutants with new cellular patterns and cell numbers might arise. It is a self-evident fact that in organisms displaying cell constancy in all somatic organs, mitotic division of the nuclei is never observed. Power of mitotic division, so characteristic of embryonic cells, is wholly lost in the differentiated cells and never again regained. Even injury, which often serves as a stimulus to resumption of mitotic activity in the production of cells for reconstruction and regeneration, is ineffectual as incentive to mitotic division in organisms displaying cell constancy. Jurczik (1927) experimentally demonstrated that regeneration does not occur in the arms of the rotifer Stephanoceros and based his explanation on the inability of the nuclei to divide. The writer has discovered what seem to have been physiological and morphological readjustments of nucleus-cytoplasm relation in two instances of organisms displaying cell constancy. One of these was in certain examples of *Hydatina senta* and the other in a phylogenetic consideration of the genera of Acanthocephala (Van Cleave, 1922 and 1928).

More than a thousand females of *Hydatina senta* have been examined critically with reference to the number and condition of the nuclei in the vitellarium. In most of these individuals, the nuclei of the vitellaria are spheroidal or ellipsoidal (Van Cleave, 1922, Text fig. a and figs. 1 and 2), but in some of the larger specimens the nuclei were irregular or elongate in shape. This change in form of the nuclei the writer has believed to be associated with morphological readjustments of nuclear surface to compensate

for physiological changes as requirements incident to the state of senescence. The same attempt at surface readjustment of the nuclei could readily terminate in the mechanical division or fragmentation of the original nuclei of the vitellaria. In fact, this is the explanation which the writer has offered for the occurrence of three individuals of Hydatina showing abnormal numbers of nuclei in the vitellarium, as mentioned earlier in this paper. If this interpretation is true, the abnormal increase in number of nuclei offers no obstacle to absolute cell constancy but represents only a senescent state of readjustment superimposed upon a condition of absolute constancy as a final phase at the close of the normal life span.

This interpretation is borne out by subsequent findings of nuclear relations in the Acanthocephala. In 1914, the writer set forth the evidences of cell constancy in the somatic organs of several species of Acanthocephala all of which are now recognized as pertaining to a single family, the Neoechinorhynchidae. In all of the members of this family, of which several thousand individuals have been studied microscopically, the nuclei of the adult worms are essentially like those of the larva at the close of the embryonic development. Even the early students of the Acanthocephala had witnessed conspicuous differences between the giant nuclei which have retained their embryonic character and those found in similar organs and tissues in species representing other genera and families of the same group of worms. The significance of this cytological difference and its bearing on the problem of cell constancy was not understood until the writer (1928) showed how the ontogenetic stages in the production of numerous small nuclear bodies in the subcuticula of certain genera (Acanthocephalus, Echinorhynchus, Pomphorhynchus, etc.) constitute an exact parallel to a phylogenetic series of nuclear conditions bridging the gap from ovoidal embryonic nuclei to finely divided nuclear masses which result from the superimposition of an indefinite amitotic fragmentation upon the large mitotically derived nuclei present at the close of the embryonic period. Thus the genera of Acanthocephala may be arranged in a phylogenetic series with the Neoechinorhynchidae and their giant nuclei at one end and those with finely divided nuclei at the opposite extreme. Genera showing intermediate conditions may be placed in linear sequence between these two extremes. Thus within the Acanthocephala there are some genera having cell constancy for all the organs and tissues, while closely related genera may have no regularity in certain tissues (the subcuticula, e.g.) because a postembryonic amitotic cycle has obliterated the constancy laid down at the close of the embryonic period. Here a condition has become established for whole genera and families similar to the senescence phenomenon observed in isolated individuals of the rotifer Hydatina.

THE TWO TYPES OF INCONSTANCY

In attempting an interpretation of the two conditions of constancy and inconstancy, two diametrically opposite possibilities present themselves for consideration. In the light of the foregoing observations on nuclei in the Acanthocephala, it is obvious that the amitotic fragmentation of the nuclei might be a coenogenetic addition to the ontogenetic process or, as alternative, that normal development ordinarily terminates with an amitotic period for the reestablishing of a new nucleus-cytoplasm ratio and in those forms having cell constancy this

condition has been attained by the elimination of the terminal amitotic readjustment.

Since the condition of constancy occurs in only those organisms having determinate cleavage and constancy is the logical projection of cell lineage into the adult state, it seems clear that the condition of inconstancy distinctive of some of the higher genera of Acanthocephala is a derived state. Cell constancy is here the primitive condition as borne out by biological evidences, and in genera showing inconstancy this condition is the consequence or introduction of new conditions into the plan of ontogeny of the Acanthocephala.

Inconstancy thus has two origins—primitive inconstancy as a consequence of indeterminate cleavage and a derived inconstancy wherein determinate cleavage lays down a basis for cell constancy which is ultimately destroyed. This offers an explanation of how cell constancy and inconstancy may occur in closely related forms, for the inconstancy here is of the derived sort.

COMMON FEATURES OF METAZOANS SHOWING CELL CONSTANCY

There are extremely few features which are held in common by all metazoans having constancy in number and arrangement of the cells. Eutely gives no more proof of phylogenetic relationship than any of the numerous homologies in structure and identity in plan of development which run through the entire animal series. One feature which all forms having cell constancy hold in common is the fact that they are restricted to the sexual type of reproduction in the formation of new individuals. This is a necessary limiting condition to constancy, for asexual reproduction can not be performed except when at least some of the somatic cells are endowed with the power of recreation so that a new individual may be fashioned out of a portion of the body of the parent. The significance of this elimination of one of the common forms of reproduction becomes evident when we remember that many of the species showing eutely are parasitic in habit. Increased power of reproduction is one of the first requisites encountered by the organism in its adjustment to the parasitic habit. Yet Acanthocephala, Nematoda, and Trematoda have all independently become successful parasites in spite of the handicap which cell constancy has imposed upon some of their members or at least upon certain stages in development, in the elimination of one of the surest avenues to rapid multiplication. Parthenogenesis, the second means of attaining a rapid rate of reproduction, offers no prohibition to cell constancy. Rotifers, insects, and trematodes enjoy the biological advantages of parthenogenetic reproduction without altering the plan of constancy distinctive of normal cleavage in true sexual reproduction.

No single statement can be made that will express a fixed relation between body size and cell number. There is no single natural law governing this relationship. In forms having cell constancy, body size is controlled directly by the size of the component cells. This is just as much a sound biological principle based upon incontrovertible evidence as is the alternative conclusion that in some other organisms body size is a function of cell number. The two conditions of constancy and inconstancy in number of cellular elements reflect neither fundamental phylogenetic bonds nor barriers, for variability in cell numbers within a given species may be either primitively the outcome of indeterminate cleavage or secondarily attained.

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SENESCENCE, AN INHERENT PROPERTY OF ANIMAL CELLS

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IN PUBLICATIONS (1a, b, c, d) from these laboratories we are trying to throw light on the problems of old age and death and of acclimatization. The view has been advanced that old age is associated with marked decrease in the catalytic activity of the body enzymes and cells. Consequently it is expected that in old age there is an appreciable decrease in the metabolism of the animal body. Observations on the metabolism of human beings of different ages show that the metabolism expressed per square metre or kilogram is less in old age than in childhood or youth. Animal life is assumed to depend esssentially on the activity of the cells and the enzymes.

The phenomenon of ageing is common to both inorganic and organic colloids and precipitates. It has been shown that the activity, adsorptive power, stability and viscosity of hydrophobe colloids, in general, decrease and the electric conductivity increases with time. On the other hand, with hydrophile colloids like vanadium pentoxide and ceric hydroxide, the hydration tendency and viscosity increase with time up to a limiting value and then decrease, and this behavior is likely to depend on the chemical affinity of these substances for water. When the chemical affinity for water is satisfied and the maximum hydration and viscosity are reached, the particles on further ageing begin to agglomerate and partially lose their adsorptive power, stability and hydration tendency. Gelatin and albumin behave like the above two inorganic hydrophile colloids.

Senescence or growing old is generally considered to be the precursor of "natural" death. There is considerable difference of opinion regarding the phenomenon of senescence amongst the biologists. Raymond Pearl (2), Woodruff (3) and others maintain that senescence appears in the multicellular body as a whole, because of the fact that the multicellular body is a differentiated morphologic and dynamic organization. The following lines from Raymond Pearl's "The Biology of Death," page 71, will make this point of view clear:

> If cells of nearly every sort are capable, under appropriate conditions, of living indefinitely in undiminished vigor, and cytological normality, there is little ground for postulating that the observed senescent changes in these cells while in the body, such as those described by Minot and others, are expressive of specific and inherent mortal processes going on in the cells; or that these cellular processes are the cause of senescence, as Minot has concluded.

Again on page 75 Pearl states:

> This phenomenon is reflected morphologically in the component cells. But it does not primarily originate in any particular cell because of the fact that that cell is old in time or because that cell in and of itself has been alive; nor does it occur in the cells when they are removed from the mutually dependent relationship of the organized body as a whole and given appropriate physicochemical conditions. In short, senescence appears not to be a primary attribute of the physiological economy of cells as such.

The other point of view can be gathered from the following statement of Jennings:

Thus it appears that in these organisms, nature has employed the method of keeping on hand a reserve stock of a material essential to life, by replacing at intervals the worn out material with this reserve, the animals are kept in a state of perpetual vigor not as individuals, growing old or dying a natural death. Nevertheless, a wearing out process such as might be called getting old, does occur in the structure employed in the active functions of life and these must be replaced after a time of service. So far as the conditions in these organisms are typical, deterioration and death do appear to be a consequence of full and active life; life carries within itself the seeds of death The great mass of cells subject to death in the higher animals dwindles in the infusorian to the macronucleus; this alone represents a corpse. But the dissolution of this corpse occurs within the living body. It much resembles such a process as the wasting away and destruction of minute parts of our own bodies, which we know is taking place at all times and which does not interrupt the life of the individual.

It will be shown in the following lines that each individual cell in the animal body loses its activity with time. This ageing of body cells is subject to the same laws as those governing the ageing of inorganic sols and gels.

LOSS OF ACTIVITY OF BODY CELLS AND CATALYSTS WITH TIME

(1) With the establishment of the cellular nature of the tissues it may well have been that the ultimate unit of life had been reached and that no minuter element need be considered. Indeed our doctrine of pathology is essentially a cellular one, although we realise that the cell in all cases is a vastly complicated structure within which there are elaborate mechanisms developed in almost infinite variety, and within which also we can find evidence of the accomplishment of chemical processes which in complexity and ingenuity of combination surpass anything which can be carried on in a laboratory. Now the animal cells are quite analogous in properties to the colloids and they are considered to be of a colloidal nature. It is well known that all colloids are finely divided particles with definite surface area.

In publications from these laboratories (5a, b, c) we have shown that the surface area, adsorptive power, stability and viscosity of the particles of hydrophobe colloids decrease with time. It has also been shown that the viscosity of a sol of ceric hydroxide goes on increasing with time up to a limiting value and that then it sets to a stiff jelly. Now if the jelly is kept in a stoppered bottle, the viscosity decreases and the sol becomes mobile again. The electric conductivity of the sol goes on decreasing to a minimum value and then it increases. Silicic acid sols prepared in hot and cold conditions show increased viscosity with time and on keeping the silicic acid sets to a jelly. In course of time the jelly is broken and a portion of the adsorbed liquid is given out. In some recent publications (6a, b) it has been shown that the clotting of blood is guided by the same laws as the formation of jellies of vanadium pentoxide, ceric hydroxide, silicic acid and of other organic and inorganic colloids. The syneresis that is observed with clotted blood, is really an ageing phenomenon, which is obtainable with most other gels and is due to the decrease in the free surface and the activity and hydration tendency of the particles forming the jelly. We have repeatedly observed that colloids of silicic acid, vanadium pentoxide, ceric hydroxide, etc., form transparent jellies by merely keeping them in a stoppered bottle at the ordinary temperature. In course of time, these stable jellies undergo syneresis. Exactly similar behavior is observable with blood, the only difference being that blood is far less stable than the inorganic sols; and the clotting and syneresis are quicker processes in blood than the gelation and syneresis observed with the inorganic sols.

Moreover, we have carried on detailed investigations on the coagulation and gelation of serum. Transparent and stable jellies have been obtained when serum is coagulated with glacial acetic acid, concentrated formic acid and other weak acids. Strong acids like hydrochloric, nitric, etc., yield opaque jellies, which slowly synerise on keeping. A similar ageing phenomenon is observable with animal cells and protoplasm. From ultramicroscopic observations it can be clearly concluded that amoeba consists of colloidal particles. Similar conclusions are drawn by Mott (7) from observations on living nerve cells by the same method. As a general rule, the small granules often seen in living cells do not show active Brownian movement, indicating that protoplasm is often of considerable viscosity. This is in harmony with the fact that it can often be drawn into long sticky threads.

The degenerative changes which precede the decay of cells are accompanied by a liquefaction of the protoplasm and by the appearance of small granules in active Brownian movement. These granules become larger in course of time, whilst the Brownian movement ceases, and this indicates that the protoplasm has coagulated. The protoplasm of young cells is often homogeneous, whilst that of the mature cell may show a definite structure. The immature eggs of Echinoderms are quite clear and transparent, whilst in the mature eggs Chambers (8) distinguishes two kinds of particles visible in the ordinary microscope—very small ones and larger ones, Macrosomes. The former are stable and the latter very sensitive to injury. It appears, therefore, that the protoplasm of young cells behaves like a freshly prepared colloidal solution and in the mature egg partial separation of the solid and increased opacity are observed due to ageing. This behavior of protoplasm is similar to that observed with a sol of silicic acid.

Fischer has shown that the same type of change takes place with proteins. Gelatine jelly, as well as other protein media, as the familiar blood serum of the bacteriologists, all squeeze off fluid on standing. The more highly hydrated the protein gel or jelly, the more liquid is squeezed off on ageing. It is well known that the percentage of water which enters into the composition of the animal body decreases with age as follows: A three months' fetus contains 94 per cent water; at birth the water content varies from 69 to 66 per cent; in adult life 58 per cent. It is held that the water content decreases in old age. Turgescence in general, and that of the skin in particular, is obviously lost. With ageing there occurs shrinking. From our experience on sols and gels we know that ageing of a sol or gel is always associated with its dehydration. Hence it appears that in course of time the body colloids have a tendency to lose their adsorptive power and activity. This is one of the important factors that lead to old age and death. The cells of the tissues are like other living things dependent for their life and activity upon a constant and abundant supply of food and oxygen and an equally adequate removal of their waste products. Now the utilization of food and oxygen is possible because of the presence of the enzymes and the surface on the cells. In course of time the activity of the enzymes as well as that of the cells is decreased and hence the metabolism is decreased.

We have repeatedly observed that the chemical reactivity of a freshly precipitated substance is much greater than that of a substance prepared long ago. Thus when ferric hydroxide, chromic hydroxide, etc., are freshly precipitated,

they dissolve very readily even in dilute hydrochloric acid; whilst the same substances prepared in the same manner and placed at the ordinary temperature in a flask even in contact with water lose much of their chemical reactivity and do not dissolve in dilute hydrochloric acid; even concentrated hydrochloric acid dissolves these old samples of hydroxides with difficulty. The adsorptive power of these substances decreases considerably on ageing. Moreover we have shown that the catalytic decomposition of hydrogen peroxide due to the presence of manganese dioxide is much greater when it is freshly precipitated than when the same weight of an old sample of manganese dioxide is used. The generation of oxygen is much greater in the same time with a fresh sample of manganese dioxide than with an old sample. Just as freshly precipitated manganese dioxide is more reactive as a catalyst in the decomposition of hydrogen peroxide, similarly the enzymes and cells in the body of a child or a young man are likely to be more reactive than the enzymes and cells in the system of an old man. As the animal or individul grows older and older, the amount of oxidation per unit weight of its body becomes less and less, as the enzymes and cells become more and more aged and inactive. Comparative experiments on the standard metabolism at different ages show that when calculated per kilogram or square metre of the body surface, the metabolism of growing individuals is greater than that of adults and in old age there is a distinct decrease. It is well known that Dony-Henault prepared artificial laccase, which is an oxidizing enzyme, by alcoholic precipitation of a solution containing gum arabic, manganese formate and sodium bicarbonate. This artificial laccase is an adsorption complex with gum and manganese hydroxide. This artificial enzyme will age in course of time and partly lose its activity.

In publications from these laboratories (9a, b, c, d), we have shown that ferrous and ferric salts and colloidal ferric hydroxide can act as active catalytic agents in oxidation reactions. Thus the oxidation of tartaric acid, starch, etc., by hydrogen peroxide can be largely increased by ferric or ferrous salts or colloidal ferric hydroxide and in this way we have explained the internal use of iron in medicine. It is well known that blood contains iron probably in the colloidal condition and that a good deal of oxidation of food materials takes place in blood. It seems likely that in course of time, the iron compound present in animal blood loses a part of its catalytic influence and the amount of oxidation in the animal body is likely to decrease with age.

Moreover the inorganic salts which are present in the body as adsorbed by the protein matter are likely to be partly given up due to the ageing of the protein particles. The body cells, enzymes, internal secretions, etc., are likely to act with the help of the adsorbed inorganic and organic substances, but in course of time, the adsorbed substances are given up and hence the activity of the cells, enzymes, etc., will decrease. The cartilages, connective tissues, bone cells, etc., which consist mainly of calcium phosphate and carbonate, will also age with time and partially lose their activity and adsorptive power. In a previous publication (10), I have advanced the view that bone formation takes place by the adsorption of calcium phosphate and carbonate existing in the colloidal state in the body fluids by the solid or semisolid cartilages, bones, etc. With time, the adsorbents, like cartilages, bones, etc., will partly lose their adsorptive capacity

and will not be able to adsorb the requisite amounts of sols of calcium phosphate and carbonate from the body and hence bone formation is difficult in old age.

From the foregoing considerations, it will be clear that the phenomenon of ageing appears to be inherent with body colloids and cells and hence senescence of the body cells is a natural phenomenon. Hence it follows that the conception of the potential immortality of each individual cell, as advocated by Raymond Pearl and others of his school of thought does not seem to fit in with the general behavior of colloids and catalytic surfaces. As has been already pointed out, the metabolism of old animals per kilogram weight is less than that of young individuals of the same species. This clearly shows that the body cells and catalysts lose their activity with time.

INFLUENCE OF TEMPERATURE ON THE AGEING OF BODY CELLS

(2) We have repeatedly observed that a freshly precipitated sample of ferric hydroxide, chromium hydroxide, hydrated manganese dioxide, etc., loses its chemical reactivity more readily when kept at a higher temperature even in contact with water than when kept at low temperature in contact with water. We have observed that the amount of adsorption of arsenious acid by a definite weight of ferric hydroxide kept at a temperature of 50° in contact with water is much less than the adsorption of the same substance by the same weight of ferric hydroxide kept at a temperature of 25° in contact with water. In other words, the decrease in the chemical activity of these substances or the ageing of these substances is more marked and rapid when the substances are kept at a higher temperature. We have observed that the precipitate of ferric hydroxide obtained by the hydrolysis of ferric chloride at the boiling temperature does not dissolve easily even in concentrated hydrochloric acid, although ferric hydroxide obtained by the coagulation of a sol prepared at the ordinary temperature dissolves even in dilute hydrochloric acid. Moreover, we have observed that manganese dioxide loses its catalytic activity towards the decomposition of hydrogen peroxide more rapidly when kept at a higher temperature than at the ordinary temperature. It seems probable, therefore, that the life period of the enzymes and other catalysts and cells should decrease more readily when the animal lives in a warmer climate than in a cold country. Consequently it appears that old age and death would take place more quickly in warmer climates than in colder ones under otherwise identical conditions especially with cold blooded animals.

From our experiments on the coagulation of sols at different temperatures, it is clear that the stability of several sols decreases considerably by increasing the temperature of the colloid. The colloids age more rapidly at high temperatures.

INCREASED RATE OF DECAY OF BODY CELLS AND CATALYSTS WITH INCREASED INTENSITY OF THEIR ACTIVITY

(3) Rubner concluded from his experiments that metabolism in different warm blooded animals was nearly constant when expressed per square metre of the body surface and we have shown that this generalisation of Rubner can be deduced from Stefan's law of radiation (11). It is evident that the amount of heat per unit weight of the body lost by an animal due to radiation is greater, the smaller the size of the animal. Hence the cells, enzymes and catalysts in smaller animals are more reactive than the catalysts and

cells in larger animals. In other words, we are led to the conclusion that the physical activity and the amount of oxidation per unit weight of the body are much greater in the case of a dog than in the case of a man. Even a most casual observation of the domesticated animals show that as a rule small animals do not live so long as large ones. Hence small animals with intensive metabolism live a relatively short time, larger animals with more sluggish metabolism live a longer time. We have already mentioned that Rubner's view is that a definite amount of living action or energy transformation determines the physiological end of life.

Sabatier and his colleagues have shown that when metallic nickel, which is used as a catalyst in hydrogenation processes, is prepared at low temperatures, the activity of the catalyst is extremely great but that it loses its activity very readily. From our experience with other catalysts we know that an extremely active catalytic surface deteriorates rapidly. Consequently it seems probable that in the biological processes of metabolism extremely active catalysts lose their activity more readily than moderately active catalysts. In this connection the following experiments of Slonaker (12) on rats will be of interest. He kept four albino rats in revolving cages with a properly calibrated odometer attached to the axle so that the total amount of running which they did in their whole lives could be recorded. It was observed that on an average each rat ran 5447 miles in the course of its life and the four rats attained an average age at death of 29.5 months. But three controlled rats confined in stationary cages, so that they could move about only to a limited extent, but otherwise under conditions, including temperature, identical with those in the revolving cages, attained an average age at death of 40.3 months. From this experiment it appears that the greater the total work done or total energy out-put the shorter the duration of life and vice-versa.

In a publication from this laboratory we have applied Stefan's law of radiation in explaining the increase in metabolism observed when the surrounding temperature of a warm blooded animal is reduced. We have advanced the view that the effect of transportation of a warm blooded animal from a comparatively warmer climate to a cold climate will be to activate the enzymes and cells in the body and that it will lead to the shortening of the life period of the animal. On the other hand, the transportation of a warm blooded animal from a very cold climate to a comparatively warm country is to cause the body cells and enzymes to work at a slower speed, and the life of the animal may be prolonged by this transportation.

From our experiments on the coagulation of sols it is observed that the stability of several colloids decreases considerably by increasing the temperature of the colloids, which will age more rapidly at the higher temperature. The body temperature of warm blooded animals is normally much higher than the surrounding air. In the case of some birds, rabbit and dog, it is higher than that of a human being. It is clear, therefore, that several of the body colloids, cells, and enzymes present in these animals will age more readily and become unstable at a moderately high temperature. Moreover, these cells and catalysts are made to work at a high speed in order to make up for the heat lost in radiation and other sources. Consequently the longevity of these warm blooded animals cannot be as high as that of cold blooded animals. Moreover, the colloids present in cold blooded animals will have longer duration of healthy life

and this leads to the greater longevity of the animals themselves.

Voit gives the following results on the influence of temperature on the metabolism of a fasting man: Temperature, 4.4°, 6.5°, 9°, 14.3°, 16.2°, 24.2°, 26.2°, 30°; CO_2 excreted in grms., 210.7, 206.0, 192.0, 155.1, 158.3, 166.5, 160.0, 170.6.

It appears from the above results that when the outside temperature is about 15° the metabolism is the minimum. Similar results showing that the metabolism is minimum when the external temperature is about 15° have been obtained with other warm blooded animals. We are of the opinion that the longevity of an animal is increased if the body cells and enzymes are made to work at a minimum speed. Moreover at 15° the body colloids do not age rapidly. Hence this temperature is the most suitable one for the healthy life of warm blooded animals. People living in a country under suitable hygienic conditions should have the maximum longevity provided the temperature of the country is near 15°.

It is well known that cold blooded animals live much longer than warm blooded animals of the same size, because the catalytic activity of the cells and enzymes present in cold blooded animals is not as great as those in warm blooded animals. When a cold blooded animal living in a warm country is taken to a cold country, the metabolism will decrease and the animal leads a life of less intensity and greater duration. On the other hand, by the transportation of a cold blooded animal from a cold to a warm country, the activity of the cells and enzymes is increased. This leads to a shortening of the life period of the animal. In this connection the following experimental results of Loeb and Northrop (13) on *Drosophila* (fly)—a cold blooded insect—will be of interest.

Effect of temperature on duration of life of *Drosophila*

Temperature.....	10°	15°	20°	25°	30°
Total duration of life in days from egg to death....	177.5	123.9	54.3	38.5	21.15

It follows from the above table that at the lowest temperature, the duration of life is longest and at the highest temperature, shortest. Cold decreases the intensity of living for the fly. Increase of temperature hastens the living process. From the account of the experiments of Loeb and Northrop, it is seen that at low temperatures the flies are sluggish and inactive and live a long time because they live slowly. At higher temperatures the flies are very active and live at a pace that kills. Similar results have been obtained by Raymond Pearl (14) in his experiments on longevity. A long series of experiments have been summarised on the duration of life in *Drosophila melanogaster* and in seedlings of *Cucumis melo*. The duration of life (longevity) of the individual varies inversely as the rate of energy expenditure in metabolism. The faster an organism lives the sooner it dies.

SUMMARY

There is considerable difference of opinion among biologists regarding senescence and death. In the foregoing pages evidence has been adduced to show that senescence or "getting old" is an inherent property of animal cells, contrary to the views of Raymond Pearl and others.

1. The author has shown that various colloids gradually lose their adsorptive power, hydration tendency, stability and other properties on keeping. In the same way, various catalysts lose their activity in the process of time. The cells and catalysts in the animal body resemble the

colloids and catalysts of the physical chemist, in the manner in which they lose their reactivity with time. Thus comparative experiments on the standard metabolism at different ages show that, when calculated per kilogram of body weight, the metabolism of growing individuals is greater than that of adults and in old age there is a distinct decrease.

2. This resemblance can be pushed further: Colloids and catalysts lose their stability and reactivity more quickly when kept at a higher temperature than when kept at a lower temperature. The animal cells show a similar behavior. The results of Loeb and Northrop on *Drosophila* (fly) support these conclusions. The life-period of this insect diminishes with the increase in temperature.

3. Moreover, Sabatier and coworkers have shown that sluggish catalysts have a longer life period than the more active ones. Similarly with the animal cells and catalysts there is an increased rate of decay and hence a shortening of their life period with an increase in the intensity of their activity. Thus, in experiments on the duration of life of *Drosophila melanogaster* and in seedlings of *Cucumis melo*, Raymond Pearl has shown that the longevity of the individual varies inversely as the rate of energy expenditure in metabolism. The faster an organism lives the sooner it dies. This is also supported by the experiments of Slonaker on rats. Moreover, it is well-known that cold blooded animals live longer than warm blooded animals of the same size, because the intensity of the catalytic activity of the cells and enzymes in cold blooded animals is not so great as that of the warm blooded ones.

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A CRITIQUE OF CERTAIN EARLIER WORK ON THE INHERITANCE OF DURATION OF LIFE IN MAN

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IN A previous paper (1) the writer published a series of life tables for a southern Chinese family from 1365 to 1849, based upon the genealogical records of that family. At present an attempt is being made to utilize the same material for studying the influence of heredity on the duration of life (2). In order to scrutinize critically the ideas on the selection of data and the method of study, a survey of the literature in this field has been undertaken under the guidance of Professor Raymond Pearl. Such a review naturally began with the well-known works of Karl Pearson and his student, Mary Beeton (3, 4), and of Alexander Graham Bell (5).

For the sake of simplicity in discussion, it seems desirable to consider Bell's study first, although Beeton and Pearson's work appeared nearly twenty years earlier.

BELL'S STUDY OF THE HYDE GENEALOGY

The data of Bell's study were taken from the Genealogy of the Hyde Family by Reuben H. Walworth (6) in 1864, relating to the descendants of William Hyde of Norwich, Connecticut, who died in 1681. Bell found 8,797 persons mentioned in this family record, and in 2,965 of them the age at death stated. Except for giving a frequency distribution by the period of birth of all persons included in the genealogy, he dealt exclusively with the group whose ages at death were known, since he was particularly interested in the duration of life and factors influencing longevity. He first described some of the bio-statistical records of these people and then compared the duration of life of persons with respect to that of their parents; the ages of their parents at marriage; the ages of their parents when the persons were born; the number of years after the marriage of their parents the persons were born; and the number of siblings in the family.

Bell's general analysis of age at death permits an examination of the material used in his investigation as to whether it represents an unbiased collection of data suitable for the purpose in view. To anyone who is familiar with vital statistics, the frequency distribution of deaths by each year of life, as given by Bell, must appear proportionally far too low in infant deaths and heavily loaded with persons who died in childhood and adult life. This overloading of young-dying persons is so excessive that the usual second mode of the death curve at the age of 70–80 is shifted to the early age of 20–25. A comparison as shown in Figure 1 of Bell's death curve with the d_x function of a life table population will help one to get an idea of the extent of disproportion. To account for this difference, it may be worth quoting Wilson and Doering's (7) comments on Bell's work in this respect:

> It may be remarked that the extreme span of life is about 100 years, that the Hyde Family was printed

in 1864, and that persons born subsequent to 1764 had not a fair chance to live out their lives. Further if we allow 30 years to a generation we may say roughly that children of parents born subsequent to 1734 had not a fair chance to live out their lives. Unhappily, of the 8,797 persons in the Hyde family only a small fraction were born prior to 1750 (869 or 9.9%). The temptation to take all material, particularly when it increases rapidly in time, leads one to include more recent births in large numbers and of

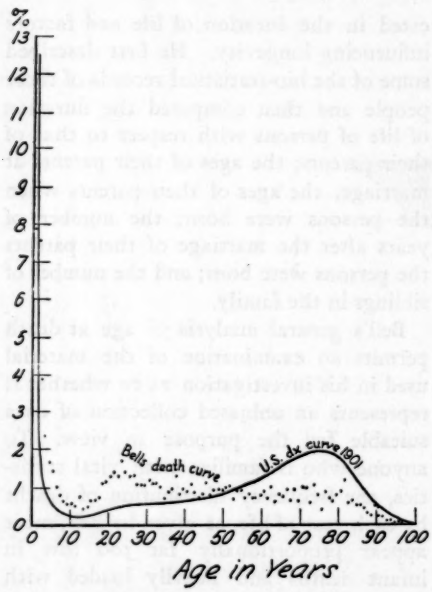

FIG. 1. SHOWING THE EXTREMELY LOW PROPORTION OF INFANT DEATHS AND THE OVERLOADING OF YOUNG-DYING PERSONS IN BELL'S DEATH CURVE OF THE HYDE FAMILY AS COMPARED WITH THE d_x CURVE (GLOVER) FOR THE ORIGINAL REGISTRATION STATES IN 1901, BOTH SEXES

these the persons themselves and still more their children, not having the chance to live to extreme old age, must of necessity give recorded ages at deaths only for those who have died relatively young.

Undoubtedly, what these authors have said is sound and gives an explanation of the overloading of young-dying persons in Bell's death curve of the Hyde family. The result of this is that a higher proportion of very short-lived children were, in Bell's analysis of inheritance of longevity, allotted to short-lived parents than to long-lived parents. This necessarily reflects upon the significance of Bell's striking finding that if both parents live to be 80 the average age at death of the children is 53, but if both parents die under 60 the average age at death of the children is 33. However, it must be remembered that in his study of the duration of life Bell made use of only persons of known age at death, who constitute not more than one-third of the total number of persons included in the Hyde genealogy. Since 2,332 persons were born prior to 1775 and only a very few of them would have remained alive by 1864, it is likely that a large part of the 2,965 persons of known age at death came from this group.

Bell's main findings on the inheritance of the duration of life from parents to offspring may be briefly summarized as follows:

1. The proportion of offspring having fathers who lived to 80 and over was 20.6 per cent among those who died young—between 20 and 40. This percentage increased with the increased age at death of the offspring, up to 46.0 when the latter increased to 80 and over. The same trend was found for persons having mothers who lived to 80 and over. (See Tables 1 and 2).

2. Where both parents lived to 80, 20.6 per cent of the offspring lived to 80 and over, in contrast with 9.8 per cent where only one parent (and not the other) lived to 80, and only 5.3 per cent where neither parent lived to 80. Where the father (and not the mother) lived to 80, 11.3 per cent of the offspring lived to 80 and over as compared with 7.7 per cent where the mother (and not the father) lived to 80 and over. These results seem to indicate that, in this material, inheritance

of longevity was more intense from the father than from the mother. (See Table 3.)

3. Where both parents died under 60, the offspring, on the average, lived only 32.8 years, while where both parents lived to 80 and over the offspring on the average lived 52.7 years. Where the parents died at the intermediate age-

TABLE 1

Number and percentage of persons having fathers who lived to 80 years of age and over (Bell)

PERSON'S AGE AT DEATH	TOTAL NO. OF PERSONS	PERSONS HAVING FATHERS WHO LIVED TO 80 AND OVER	
		Number	Per cent
0–19	669	161	24.1
20–39	538	111	20.6
40–59	467	124	26.6
60–79	428	162	37.5
80 and over	185	85	46.0

TABLE 2

Number and percentage of persons having mothers who lived to 80 years of age and over (Bell)

PERSON'S AGE AT DEATH	TOTAL NO. OF PERSONS	PERSONS HAVING MOTHERS WHO LIVED TO 80 AND OVER	
		Number	Per cent
0–19	511	95	18.6
20–39	407	85	20.9
40–59	379	101	26.6
60–79	360	125	34.7
80 and over	148	60	40.5

periods, the average duration of life of the offspring was intermediate. (See Table 4.)

In view of Bell's neglect to exclude from his material deaths of parents and still more their children who had not had the chance to live to the full span of life by 1864, more young-dying children must have been allotted to short-lived parents and, consequently, the average duration of life of their children calculated from his data must be necessarily lower than the true normal average. One should therefore keep in mind this fact in interpreting Bell's quantitative findings on the inheritance of the duration of life, although one probably would not hesitate to agree that Bell had demonstrated an important influence of heredity upon longevity.

TABLE 3

Number and percentage of persons dying at 80 and over as compared with longevity of their parents (Bell)

AGE AT DEATH OF PARENTS	NUMBER OF PERSONS	NUMBER OF PERSONS LIVED 80+	PERCENT OF PERSONS LIVED 80+
Lived to be 80+:			
Neither parent	827	44	5.3
One parent (not other)	583	57	9.8
Both parents	184	38	20.6
Father (not mother)	337	38	11.3
Mother (not father)	246	19	7.7

TABLE 4

The average duration of life of the offspring for various ages at deaths of both father and mother (Bell). (The bracketed figure is the number of cases on which the average of life duration is based)

FATHER'S AGE AT DEATH	MOTHER'S AGE AT DEATH		
	Under 60	60–80	Over 80
Under 60	32.8 yrs. (128)	33.4 yrs. (120)	36.3 yrs. (74)
60–80	35.8 (251)	38.0 (328)	45.0 (172)
Over 80	42.3 (131)	45.5 (206)	52.7 (184)

Among Bell's studies of conditions associated with longevity, it may be of interest to note his finding that the youngest parents at the time of birth of their children, on the average, had the longest lived offspring. The actual figures are shown in Tables 5–6. The persons whose fathers were under 25 when the persons were born lived to 39.6 years on the

average. The average duration of life decreased continuously down to 31.5 years where fathers were 40–45 when the persons were born. For the corresponding age periods of the mothers when the persons were born, the average duration of the persons changed from 38.7 to 28.1 years.

It may be pointed out that the persons whose fathers or mothers were under 25 when the persons were born had a similar duration of life as those whose fathers and mothers both lived to 60–80. Not very many persons are so lucky as to have both parents live to 60–80 and none of the offspring can choose their parents, but the chance of being born when either parent is under 25 is good and can be more or less controlled by parents. Here seems to be a condition influencing longevity deserving further investigation, as, for reasons already stated, no great confidence can be placed in Bell's figures, which are subject to the same error of the differential cutting off of the later generations as his finding on the inheritance of longevity. Children born when their parents were older were on the average born in a later calendar year than those born when their parents were young, and had therefore in later generations less time in which to live out their lives. This would spuriously decrease the observed duration of life of the later born, and therefore renders Bell's conclusion doubtful.

TABLE 5

The average duration of life of the offspring for various ages of fathers when they were born (Bell)

FATHER'S AGE WHEN PERSON WAS BORN	NUMBER OF PERSONS	AGGREGATE YEARS LIVED	AVERAGE YEARS LIVED
Under 25	180	7,132	39.6
25–29	601	23,000	38.3
30–34	642	23,640	36.8
35–39	572	19,747	34.5
40–44	409	12,894	31.5
45–49	235	7,383	31.4
50 and over	126	3,997	31.7

TABLE 6

The average duration of life of the offspring for various ages of mothers when they were born (Bell)

MOTHER'S AGE WHEN PERSON WAS BORN	NUMBER OF PERSONS	AGGREGATE YEARS LIVED	AVERAGE YEARS LIVED
Under 25	525	20,322	38.7
25–29	603	22,073	36.6
30–34	561	18,829	33.6
35–39	422	14,161	33.6
40 and over	275	7,731	28.1

In conclusion, Bell says:

> The statistics indicate that a tendency to longevity is an inheritable characteristic, capable of being handed down from parents to children.
>
> What is really inherited is probably a tough, wiry constitution that enables the possessor to survive the multitudinous ills that flesh is heir to and live on to the extreme limit of human life. From this point of view the attainment of old age is extremely significant. The last survivors of a whole generation are people who have by the very fact of their surviving to old age proved themselves to be resistant to disease. They have been exposed to the diseases and accidents that have cut off the vast majority of their fellows before their prime, but have not succumbed.

These conclusions are probably correct, but they cannot be said to have been established by Bell's work.

BEETON AND PEARSON'S WORK ON ENGLISH DATA

Beeton and Pearson collected their material from several sources. In their first study, three series of data were taken from the English Peerage and Landed Gentry. Owing to the limitations of the material, they dealt with only the adult males of 20 years of age and over. The second study was based upon more extensive pedigree records of the members of the English Society of Friends and of the Friends' Provident Association. They

included both males and females of all ages. Using such data, these authors attempted to measure by the method of correlation the intensity of inheritance of the duration of life, not only in the direct line of descent but also in the siblings.

Concerning the homogeneity of the material used, an inspection of the correlation tables given by Beeton and Pearson of sons dying at 20 and over with the figures for Massachusetts males in 1890 of the corresponding age groups and found that the former in the early adult age groups had almost twice as many as the latter. What effect these deviations from a normal general population might have had on their coefficients of correlation it is difficult to say without actual calculation from more homogeneous material, but the average ages at death as determined by these English authors would necessarily be altered.

TABLE 7

Correlation of the duration of life between the offspring and parents and between siblings (Beeton and Pearson)

RELATIVES		CORRELATION COEFFICIENT r_{xy}
x	y	
Father	Adult son	0.135 ±.021
Father	Minor son	.087 ±.022
Father	Adult daughter	.130 ±.020
Father	Minor daughter	.052 ±.023
Mother	Adult son	.131 ±.019
Mother	Minor son	.076 ±.024
Mother	Adult daughter	.149 ±.020
Mother	Minor daughter	.138 ±.024
Elder adult brother	Younger adult brother	.229 ±.019
Adult brother	Adult brother	.285 ±.020
Minor brother	Minor brother	.103 ±.029
Adult brother	Minor brother	−.026 ±.025
Elder adult sister	Younger adult sister	.346 ±.018
Adult sister	Adult sister	.332 ±.019
Minor sister	Minor sister	.175 ±.031
Adult sister	Minor sister	−.026 ±.029
Adult brother	Adult sister	.232 ±.015
Minor brother	Minor sister	.144 ±.025
Adult brother	Minor sister	−.006 ±.035
Adult sister	Minor brother	−.027 ±.033

Pearson indicates that, just as in the case of Bell's material, the death distributions fail to include infant deaths in large numbers, but are overloaded with young-dying persons. In none of these death distributions is the recorded number of deaths during the first year of life twice that for those dying in the second year of age. The usual ratio is four times or more. Wilson and Doering compared the frequency distribution given by Beeton

Beeton and Pearson's method of investigation is the same in both of their studies and the various values of correlation coefficients of their second study are given in Table 7. They separated deaths into those dying as adults and those dying as minors by taking the age of about 20 years as an arbitrary line of demarcation

in order to measure separately the intensity of what they have called the inheritance of "brachybioty" as well as that of longevity. The upper portion of Table 7 gives the results between parents and offspring, and the remainder those between the siblings. They found that the correlation in the duration of life was greater between two brothers or two sisters, than between brother and sister; between father and son and mother and daughter, than between father and daughter or mother and son. The daughter seemed to be more closely related in duration of life to her parents than the son.

TABLE 8

Average age at death of adult siblings where a sibling has died (Beeton and Pearson)

IF THERE HAS DIED	AVERAGE AGE AT DEATH	
	Adult brother	Adult sister
Adult elder brother	54.575	57.209
Adult younger brother	58.560	
Minor brother	49.009	46.135
Adult elder sister	58.804	55.667
Adult younger sister		59.924
Minor sister	48.201	50.300

TABLE 9

Average age at death (Beeton and Pearson)

IF THERE HAS DIED	OF ADULT BROTHER	OF ADULT SISTER
Infant brother	50.116	46.027
Infant sister	47.830	50.236

The general effect on the duration of life of an adult produced by the death of a brother or sister in their minority seems noteworthy and is shown in Table 8.

Table 8 shows that the death of his sister as a minor seems more important to a man than the death of his brother as a minor, and *vice versa* for a woman. Beeton and Pearson then went on to find out whether siblings if lost before 11 years of age were responsible for this result. Table 9 shows the result. It is suggested that some diseases to which a family might be prone were liable to attack one sex in infancy and the other in adult life. But this is pure speculation.

So much for Beeton and Pearson's findings on the inheritance of the duration of life. Now, we may consider briefly the applicability of the coefficient of normal correlation in measuring the intensity of the inheritance of the duration of life. The theory of normal correlation as developed by Galton presupposes normal distribution of the variables under consideration. But the frequency curve of deaths at various ages is not in any sense normal. It begins with a J-shaped function, decreasing rapidly until the age of puberty, after which it gradually rises. Passing a couple of upward waves of small magnitude in the early adult period, the curve continues to increase, reaches its second modal point at a little over 70 years of age, and then declines fairly rapidly. Even in the latter period it is a skew curve rather than a normal one. This is probably one of the reasons why Pearson separated deaths as adults and as minors by taking the age of about 20 as an arbitrary division point in his study of the correlation of duration of life. Such a procedure, however, does not seem to eliminate the major difficulty in using the method of normal correlation to measure the intensity of the inheritance of duration of life. An examination of Pearson's correlation tables dividing deaths as adults and minors shows that none of his frequency distributions of deaths may be said to be normal. Beeton and Pearson fully realized this difficulty, but finally endeavored to dispose of it in the following words:

> It is known that the curve of frequency of death at different ages is by no means normal. It is probably

compound, and only approximates to normality round three score years and ten. It would hardly, however, fulfil a useful purpose to deal only with the correlation of ages of death of relatives both dying under old age mortality group, even if on the sunny side of 70 we could distinguish old age from middle age mortality. But in dealing with correlation and regression in such cases as this, we must throw entirely on one side any notion of normal surface and curves of error, and go simply to the kernel of the affair.

But going "simply to the kernel of the affair" seems a somewhat dashing procedure, methodologically considered. Realistically viewed it appears that the quantitative results reached by the method of normal correlation on the intensity of the inheritance of duration of life in man are not unquestionable.

SUMMARY

While the investigations of Beeton and Pearson and of Bell on the inheritance of duration of life in man merit the credit which attaches to pioneering efforts, they both have certain defects which make it impossible to accept their results, in respect of their quantitative aspects, at their face value. Both made use of relatively small and somewhat circumscribed (in respect of randomness) samples of genealogical material, the biostatistical characteristics of which were rather far removed from those of a general population. Furthermore, it appears to be open to question as to whether the method of Galtonian correlation is a reliable or valid one for the solution of this problem. Standard actuarial methods applied to material having biostatistical characteristics substantially in agreement with those of a biologically normal general population would seem better adapted to a sound attack on the problem. Certain studies along this line are in progress in this laboratory and are being reported as this paper goes to press (8).

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AESTHETIC NOTIONS IN ANIMAL BREEDING

By WALKER VAN RIPER

THE aesthetic canon with the greatest range in the modern world is: *Form follows function.* This alliteration states the whole philosophy of twentieth century architecture, and it is certainly in architecture that our present-day world is expressing itself in the most novel and vigorous manner. The idea is not exactly new. Leonardo had it when he pointed out that his newly invented flying machine would not work because it was awkward and ugly. "When it worked," he said, "it would be beautiful"—a prediction which certainly came true.

Beauty in other fields may also be attributed to functional perfection. Thus Thomson and Geddes in "Life" (17) maintain "that all living things are beautiful" and that the particular reason why animals and plants delight us so uniformly is that we see in them "harmonious unities which have stood the test of time, which have been chiselled from within by harmonious metabolism and rhythmic orderly growth." "Perfectly adaptive architecture," they continue, "from which all the useless has been eliminated, the organized ripple marks of orderly regulated growth, the color expressions of successfully rhythmic metabolism from which everything disorderly has been sifted out, *ought* to be beautiful; that is to say, they may be expected to excite pleasant physiological processes in the spectator."

Darwin (2) seemed to believe that both in man and in animals the sense of beauty was due to absolutes innately given. This instinctive feeling for what was aesthetically right was essential for the argument for sexual selection and was one of its weak points (14). Wallace's (18) view was close to modern aesthetics. He rejected the theory of sexual selection altogether. The intense coloring of the male he ascribed to the greater energy of the male as compared with his mate. It is, he held, a general rule that thin and sickly animals are dull of color, while healthy ones are of brighter hue. He suggested that natural selection plays a part here, for the stronger male will win a mate more easily, and, being strong, he will be beautiful.

NON-FUNCTIONAL STANDARDS IN BREEDING

It is a very curious, and perhaps a very significant, fact that in the breeding of domestic animals the aesthetic notions which play a very large part in determining what the breeder shall strive for and regard as beautiful and good are not based on an admiration of functional perfection. On the contrary, these ideas are often not only unrelated to function but are even positively antagonistic to it. It is the purpose of this paper to inquire into the nature of these notions, the way they originate and develop, and the character of their force and effect.

It needs no proving that every fancier and breeder of animals knows beyond cavil and in the most exact and definite way what beauty is in the particular breed he cultivates. He knows it in every detail—actually to a hair's breadth—and no artist or critic can be more dogmatic and certain and bumptious than a pigeon fancier or a dog breeder

with respect to the minutiae of beauty. Moreover, there is wide agreement among breeders and this agreement takes expression in the "standard" for the breed. In fact one of the first and most important functions of a breeders' association is to fix the standard and to get it down on paper in exact detail. These details are known as "points," or "properties."

Points are aesthetic notions. Each is a consensus of what is right and beautiful with respect to a definite situation. Moreover they carry all the authority of revelation. Something of the fancier's enthusiasm, and affection and respect for the properties of a breed is indicated in a sentence which Darwin loved to quote from John Matthews Eaton's "Treatise on the Art of Breeding and Managing the Almond Tumbler" (4): "If it was possible for noblemen and gentlemen to know the amazing amount of solace and pleasure derived from the Almond Tumbler, when they begin to understand their (i.e., the tumbler's) properties, I should think that scarce any noblemen or gentlemen would be without their aviaries of Almond Tumblers."

DYSGENIC EFFECTS OF AESTHETIC SELECTION

In a fancy breed like the Tumbler which is cultivated entirely for non-utilitarian purposes we may consider the animal's inherent capacity to vary in certain directions as the material with which the breeder works. Then within the limitations of this material what the animal becomes in fact is determined by the breeder's aesthetic notions, i.e., by his ideas of what is appropriate, right, and beautiful. As will be noted below, there are remarkably few domestic animals that are bred and selected on a strictly utilitarian and performance basis without reference to phenotypic points. Most, no matter how predominantly utilitarian in fact, are bred to a standard. And it is a fact which throws a great deal of light on the authority and power of aesthetic notions that frequently the points of a strictly utilitarian breed are positively dysgenic and detrimental. Some examples will be instructive.

One of the most striking is a general observation about the breeding of dogs. There are some utility breeds, but most kinds are bred to serve as domestic pets. Satisfactory accomplishment in this respect depends rather on temperament, intelligence, and other inner qualities like loyalty than on points relating to the outward characteristics, style, carriage, conformation, coat, etc. Yet that human management which is in fact responsible for the great variety of the breeds of dogs has always been directed toward the production of eye-appealing points rather than toward a selection on the basis of the really desirable characteristics. Of course the breeder never fails to fall into the error of correlating the outward and visible signs which he has produced with inward and spiritual grace. But the correlation occurs only by chance. An authority (8) on this subject recently said that he had been able to find only one instance of selection in dog breeding on the basis of intelligence. That was in a certain family of circus dogs.

Sporting dogs, such as pointer and setter, are tested in field trials, but, as these breeds are also shown and judged on points, what the breeder finally produces is determined in part by performance tests and in part by the fancy points adopted for the breed. This is true of other animals, particularly fowls and milk cows, which are placed in competition both in performance contests and in the show ring. Probably the only breeds of dog that are bred on performance

alone without reference to any fancy points are the working sheep-dog and the malemute.

One of the show points of the White Leghorn is yellow legs and it has been definitely demonstrated by Blakeslee (1) that the correlation between egg production, for which this breed is cultivated, and the amount of yellow pigment is inverse. The breed standards for Clydesdale and English Shire draft horses call for long hairs growing from the back of the cannons and fetlocks. The result is that these horses are useless in clayey soil districts, as, in the spring and autumn, so much mud clings to the great feathers that the horse can scarcely move.

Naturally this sort of thing occurs much more frequently with the strictly fancy breeds. Pigeons afford the best examples. The Almond Tumbler mentioned above, as well as numerous other "short-faced" varieties, has such a short bill (this being one of the properties of the breed) that the young are fed with difficulty. Hence the breeder must provide wet-nurses of another breed to bring up the young tumblers. Fantails have developed tails, the chief point of the breed, which often interfere with copulation. The result is that the breeder is forced to trim the tail feathers of his breeding stock. The Jacobin is another bird with strikingly dysgenic characteristics. The monstrous "hood" which is the mark of this breed entirely covers a Jacobin's head so that the bird can scarcely see to eat, or move, or feed its young.

To return to the utility breeds, many of the required fancy points are merely irrelevant, being neither detrimental nor related in any way to the useful characters for which the breed is cultivated. This is a matter of much more importance than appears at first thought. Eaton, the Almond Tumbler authority quoted above (4), made the point: "There are some of the young fanciers who are over covetous, who go for all the five properties at once (i.e., they try to develop all the five points of the breed at once), they have their reward by getting nothing." Darwin (3), who cited this in a letter to Huxley, commented as follows: "In short it is almost beyond the human intellect to attend to *all* the excellencies of the Almond Tumbler!" If there are difficulties in the way of cultivating simultaneously five properties in an animal as plastic and easily modifiable as the pigeon it is plain enough that in the larger and slower-growing breeds attention to irrelevant fancy points may be a serious matter, the result being to dissipate the attention of the breeder and to cause the destruction of non-conforming but actually useful animals.

In his "Breeding of Farm Animals" M. W. Harper (7) comments on this question as follows: "Many of our leading breeders have adopted breed standards that operate as a check upon the maximum development of useful characters. A very good example of this is observed in the color markings of the Dutch Belted cattle. According to this requirement every cow must first have a white belt about the body, which certainly adds nothing to her ability to produce milk. Many high-producing cows are eliminated from breeding simply because they are deficient in this character. Possibly this serves to keep the herd behind its competitors as milk-producing animals."

E. P. Prentice (13) has been able to trace the history of many of the fancy points of the Guernsey breed back through the early English writers on husbandry to the Latin authors—Vergil, Varro, Columella, and others. He has also shown the futility and harm of such fancy points appearing on the Guernsey

score-card as "horns slightly in-curved inward," "a long thin tail with good switch," "a buff-colored nose," and finally, at his Mount Hope Farm at Williamstown, Mass., he has made a convincing demonstration of the sound principles of breeding dairy cattle. The Mount Hope Bull Index, which is a method of rating breeding animals on the basis of progeny performance exactly in accord with the principles worked out by Raymond Pearl for poultry at the Maine Experiment Station over twenty years ago, has been adopted by numerous breeders' associations and will certainly grow in favor as it comes to be understood.

Other examples of irrelevant points are chestnut color in Suffolk draft horses and Hackney coach horses; the escutcheon of the Holstein-Friesian as well as the long tail and the black and white color; the black tongue of the Jersey cow; the characteristically shaped horns and straight back of the Ayrshire cow; the white belt of Hampshire swine; and the six white points in a field of black in the Poland Chinas and Berkshires.

THE EVOLUTION OF STANDARDS

The tyrannous power of these notions is comparable to that exercised by style and fashion in human dress. In fact they are doubtless of the same nature as style and fashion. They have the same aesthetic basis, are equally irrational, may either promote or oppose welfare, may be irrelevant and foolish, and they operate with the greatest authority. There is just one difference: human styles seem more capricious, may change more quickly and more often. But the reason for this is that the time element is of great importance in animal breeding and that changes in the standards must necessarily come slowly. Changes, however, do occur and if we consider how and why they occur we gain some insight into the nature of the underlying ideas.

For this purpose let us return to pigeons. Man's creative and aesthetic impulses have wrought more curiously here than in any other field of animal breeding as they have been entirely unrestrained by practical considerations. Moreover there is considerable literature available and this literature is perfectly naïve, uncritical, and unliterary and is correspondingly illuminating, particularly in its aesthetic aspects.

The first work in English on the different varieties of the domestic pigeon was John Moore's "Columbarium," 1735 (9). A careful reading of Moore's descriptions by one who is acquainted with modern standards discloses the fact that in the case of practically every breed mentioned considerable changes have been made in the two centuries since Moore made his observations. This is not very surprising. We shall confine ourselves to the developments in two breeds—Magpies and Racing Pigeons.

Robert Fulton's "Book of Pigeons" (6) was published about 1893. It is a large book, beautifully illustrated with colored plates, and will doubtless be recalled as a boyhood possession by many of the readers of this article. Fulton classes the Magpie with the German Toys and indicates that it had only recently come into considerable favor in England. The standard which he gives in detail calls for a smallish bird with a round body, shaped and carried much like that of a Tumbler. The head and beak should resemble in shape those of the Blue Rock, i.e., the head should be round with a pronounced forehead and the beak rather small, slender, and sharp. The legs are short. The color marking, from which the bird gets its name because of its resemblance to that of the magpie, con-

sists of a solid color—black, yellow, or red—contrasted with white, the white portion being the underparts and all of the wing except the shoulder. The contrast between the bird so described and the modern Magpie is almost incredible. The present-day bird retains the old markings, but in every other respect is unrecognizably different. It is a long, slender bird, with long legs, a thin body, upright carriage, a long, swan-like neck, and the head of a snake, i.e., conical with the forehead making an unbroken line with the long, heavy beak. Color aside, the contrast between the giraffe and his distant cousin, the domestic cow, is scarcely greater than that between the modern Magpie and the bird of forty years ago.

An account of certain developments in the history of the Homing or Racing Pigeon is even more instructive for our purposes. According to Moore (9) the Carrier pigeon was so named because it had originally in its Persian home been used to carry messages. But even as early as 1735 it had long since become ill adapted for this purpose and had graduated, or degenerated, into a purely fancy variety. Regarding it Moore said: "This Bird is esteem'd, by the Gentlemen of the Fancy, as the King of Pigeons, on Account of its Beauty and Great Sagacity; for which reason Mr. Hickman, a Distiller in Bishopsgate-street (not of the family of the living Hickmans) when living, always kept a silver Hatchet and Block, on which he decently chopp'd off their heads, alledging, that being of the Royal Blood, they ought not to die after the same Manner as the Vulgar Herd."

The distinguishing mark of the Carrier is the wattle which in this breed is developed to a monstrous size, so that it looks as though the long bill had been thrust through a globular, cheesy substance about the size of a walnut. This development, together with the eye ceres, which are also enormous, interferes so with the bird's vision that flight is practically impossible.

The modern Homing or Racing Pigeon is frequently called a Carrier, but this is entirely incorrect, as the Carrier is still nothing but a fancy pigeon. In fact, as the wattles and eye ceres have been further developed since Moore's day, it is even more incapable of flight than it was then. The Homer of today is a very recent breed, having been developed according to the British naturalist, Tegetmeier (16), in Belgium in the early eighteen hundreds from crosses of the Cumulet and the Smerle with possible infusions of blood from several other breeds. Owing to its cross-bred origin this pigeon is remarkably variable. It is of particular interest here because it affords a beautiful illustration of the clash of man's practical and aesthetic interests and because this conflict in turn throws some light on the nature of his aesthetic notions.

Pigeon racing is a highly competitive sport involving an animal which is easily bred in large numbers and which comes to maturity and the height of its powers in its second or third year. Moreover, the usual race program tests the endurance, speed, fortitude, and homing ability of the animal to the limit. These conditions together with the heterozygousness of the bird and its consequent variability encourage a system of breeding which is severely selective. The fact that successful racers are of all colors, sizes and shapes makes selection on the basis of performance alone, excluding all considerations of type, an obvious procedure. This involves an elimination of the influence of aesthetic notions. It should be noted that man breeds few of his animals strictly on the basis of performance—polo ponies,

the two dogs mentioned, and roller canaries are possibly the only ones in addition to racing pigeons.

But in spite of what has been said about the obviousness of using performance alone as the basis of selection in breeding Racing Pigeons man continually demonstrates in this field how incorrigibly subject he is to his aesthetic ideas and with a very curious result. We have already noted how the Carrier, originally a utility bird, entirely lost its usefulness when it came to be bred as a fancy pigeon to type and standard. In the last thirty or thirty-five years this same thing has happened three times to Racing Pigeons! It seems to happen in this way: All animal breeders like to show their animals, racing-pigeon fanciers among them. Showing involves judging, and judging necessitates a standard, express or implied. Success at a show depends on meeting the judge's ideas of the standard. When these ideas become definite, fixed, and known they become a basis on which the breeder may practice selection. If he is a racing-pigeon fancier he may begin to breed to type rather than to performance. And the final result is that within the fancy two groups are formed, one breeding to type, and the other to performance.

The process just described has no effect whatever on the real Racing Pigeon, that is, it does not modify the breed in any way. What it does do is to create an entirely new breed, this being the work of the group of breeders who breed to type. And the new breed, just as the Carrier did, becomes a fancy pigeon, entirely useless for racing. The first of these breeds to develop was the English Show Homer. The date cannot be fixed definitely, but it must have been around 1895 to 1900. There is no need to describe the bird exactly but it may be said that it is strikingly different from the Racing Pigeon, short, round-bodied, rather upright, and with a characteristically shaped head—curved and rather ocarina-like.

Next there was developed, by exactly the same process, the Exhibition Working Homer. It must be emphasized that these are entirely different breeds, quite different in appearance. The greatest difference between the Exhibition Homer and the Show Homer is in the shape of the head, that of the former being more evenly conical, more slender, and much like that of the Magpie described above. Exhibition Homers are entirely fancy pigeons, never cultivated for racing or message carrying.

The third off-shoot from the Racing Pigeon appears to be at the height of its popularity now. This breed is known as the Flying Homer, or the Likeliest Flyer. The last name is significant, as we shall point out in a moment. At present-day pigeon shows it is quite common to find more Likeliest Flyers exhibited than any other variety. This bird is at a most interesting stage of development as it has not yet quite become a non-flyer. It is difficult to predict which point will be chosen for development and enlargement as the process is completed of making the Likeliest Flyer into a fancy pigeon. The writer thinks it will have to do with the way the wings are held, projecting wing-butts being one of the points most emphasized now.

These three instances indicate how man's aesthetic impulses tend to run away with the show and thus they illustrate how deep-seated, elemental, and powerful the aesthetic notions are. But there is more than that to be learned from them. Particularly they throw light on the way the notions arise and also on the fact that, although the notions are always, at least at first, assumed to be beneficial and welfare-promoting, this may or may not

be true, being due largely to chance; yet, even when not true, that is when the notions are positively detrimental, dysgenic, or anti-utilitarian, they lose little, if any, of their force.

Certainly with the Likeliest Flyer, as the name indicates, and almost certainly also with the Show Homer and the Exhibition Homer the standards of the breed originally developed out of the attempts of judges to correlate the visible characteristics of true Racing Pigeons with racing ability. It must be realized that these attempts are very uncritical and that it makes no difference whether they are sound or not. A judge may often be a real racing pigeon fancier. In this event the ideal which forms in his mind of the perfect Racing Pigeon very naturally develops out of his own experience, i.e., he postulates as ideal the characters which appear in his own favorite or most successful birds. The writer knows from his own experience that it is practically impossible for the breeder to avoid doing this. If the judge is not a breeder he picks up his notions in some other way. We have seen a judge of racing pigeons point out with perfect confidence the bump on a bird's head that indicated intelligence. Others know with the utmost certainty what shape of bird is aerodynamically the best. And there is a Belgian cult that can tell all about a pigeon's racing ability by examining "the circle of correlation," a visible muscle surrounding the iris.

The experienced breeder always gives the novice the perfectly sound advice to find out what the judge wants and then to give it to him. This naturally makes for success in the shows and it is a bit of wisdom that appears with great frequency in the literature of animal breeding. It is probably fair, therefore, to say that the notions concerning the properties of a typical animal originate with the judges, and it must not be forgotten that the process is entirely uncritical and irrational. If there are a number of judges their tastes will differ, at first rather widely. At this point the influence of the fancy at large comes in. This influence consists in a selection of the notions which originated with the judges and a consolidation and a consensus arise which take the form of a general agreement as to the standard.

We have now seen how the aesthetic notions which direct the breeding of domestic animals originate and develop. The view presented indicates that these notions are essentially uncritical and irrational; that they are conservative and very powerful; that their power rests on the assumptions that they are right and good and truly representative of beauty and that they are really correlated with welfare and purpose. Finally we have brought out the fact that, due to the nature of the origin of these notions, it is largely a matter of chance whether they are or are not in fact welfare-promoting and that within certain limits the fact that notions are really detrimental does not diminish their authority. Inferentially also we have indicated that a truly sound method of animal breeding must be based on the form-follows-function principle to the exclusion of all the natural aesthetic notions which in fact so largely dominate. Our main interest, however, has been to examine the nature of these notions.

THE MORES

The field of animal breeding which has furnished the material for our discussion is very interesting because it affords an opportunity which is not matched elsewhere to examine a set of human ideas in origin and evolution. It is further inter-

esting because the process which we have been observing may have much wider applications than we have indicated up to this point.

Architecture, for example, may be divided, like racing pigeon breeding, into two sections, one breeding to performance where form follows function; the other breeding to type and under the domination of aesthetic notions as uncritical, irrational, and irrelevant as any of those noted above. Certain modern skyscrapers illustrate the first and almost all of domestic architecture, the second. The builder of an expensive imitation of a copy of a fake French chateau doubtless gets an aesthetic thrill out of his work which is of exactly the same nature as and not different in quality from that achieved by the breeder of Jacobin pigeons. The fake French chateau, however, can hardly be said to be positively dysgenic. It is fairly functional. Probably the most that can be said is that it is unintelligent and stupid and costs far more than it is worth.

Automobile design is another field which cannot free itself from the tyranny of irrelevant aesthetic notions. It is said (5) that an automobile designed to meet air resistance in the best way would have more than twice the efficiency of the currently accepted design. The trouble is that the customers know too well what is right, and good, and true in automobile bodies.

Other instances taken from the applied arts might be cited, but in closing we wish to raise the question as to whether the general process which we have described may not go even further than this. William Graham Sumner in "Folkways" (15) has shown how social and political institutions grow out of the *mores*. And he defines *mores* as the notions and ways of doing things which have acquired the quality of being regarded as right, and good, and beautiful. He shows the conservative character of the *mores*, develops the fact that they are assumed to be conducive to welfare while in fact they are irrational, often irrelevant, and may or may not be welfare-promoting. Out of the *mores* institutions, laws, and philosophies evolve. We connect these things with the names of leaders who are supposed to have created them. But all that the leaders really do is to rationalize the notions which the *mores* created or were. The aesthetic notions which we have had under consideration in this paper are minor *mores*. To understand their nature, how they arise and develop, is interesting because this may afford some insight into the character of other notions of greater importance.

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THE RECAPITULATION THEORY

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(Contribution from the Zoological Laboratories, University of Illinois, No. 419)

HAECKEL'S fundamental biogenetic law or the theory of recapitulation, as it is more generally called, has been the subject of discussion for over sixty years. During this time it has found its way into all elementary textbooks on biology and has often been treated as one of the most important biological generalizations. But it has not been altogether free from attack during this period and the objections to its acceptance are now more widespread than ever before. The great weight which has been attached to this theory in speculations concerning the phylogenetic relationships of the invertebrate animals, and in comparative vertebrate organogeny, would alone serve to demand a reëxamination. De Beer's lively review of this topic (1930) prompts me to renew my own doubts as to the validity of the recapitulation theory, especially in the light of modern developments in genetics and experimental embryology.

The historical antecedents of Haeckel's theory are ably reviewed by Russell (1916), who draws a happy distinction between the theory of parallelism, especially as developed by Meckel (1811) and by Serres (1834), the theory of divergence enunciated by von Baer (1828), and the Haeckelian theory of recapitulation (1866).

The theory of parallelism, based on the Aristotelean idea of a scale of beings, held that in the development of the higher animals there is a succession of stages which correspond to the succession of adult types in the ideal scale of beings. In its most extreme form this theory would imply that the lower animals were permanent embryos of higher forms.

It is sometimes forgotten that von Baer's position was in direct opposition to the theory of parallelism. It is an ancient scandal that Haeckel in citing von Baer's conclusions to support his own theory deliberately suppressed the fourth: "Fundamentally the embryo of a higher animal form never resembles the adult of another animal form, but only its embryo" (Russell trans.). The theory of divergence is that the general characters of a large group of animals appear in the embryo earlier than do the special characters and that there is a succession of stages from the most general to the most specific.

The theory of recapitulation attempts to combine these two points of view by making use of the theory of evolution. Recognizing the divergence shown in the developmental history of different animals, Haeckel sought to explain this as due to a corresponding divergence in the evolutionary history of the adult types. The similarities in early stages he considered the result of a common ancestry. The dissimilarities found in later stages he thought were due to the different lines of genealogical descent. Failures to find adults corresponding to well marked embryological stages he attributed to the extinction of ancestral species in the struggle for existence. But these ances-

tral forms, he believed, might be reconstructed from the data of comparative embryology.

Attempts to make the data of embryology fit the hypothesis of recapitulation revealed obvious discrepancies, some of which were recognized by Haeckel himself. Thus he pointed out that the time element would be effective in modifying the historical record through the necessary condensation of an evolutionary succession into the relatively brief period of individual development. Many evolutionary stages must be omitted entirely, others will be greatly abbreviated, and so the result must be explained as a recapitulation rather than a repetition. He noted further that many embryonic structures possess an embryonic rather than an adult value and so may not be available for phylogenetic interpretations. These he looked upon as interpolations or falsifications of the record and was led to a formal distinction between ancestral (recapitulatory) structures as palingenetic characters, and embryonic (or larval) adaptations as caenogenetic characters. This distinction, by the way, is difficult to draw in actual practise and has resulted chiefly in acrimonious debate. But with these exceptions duly noted, the adherents of the Haeckelian dogma have insisted that the *sequence* of embryonic development affords the principal clue to the sequence of evolutionary succession.

HETEROCHRONY

But even this residuum of recapitulation has not met with universal acceptance. Keibel (1897) among others called attention to apparent reversals of sequence in development. Thus among the vertebrates teeth are structures much older in evolution than the tongue but in the development of mammals the tongue appears before the teeth. De Beer lists no fewer than eight possible classes of such disturbances in sequence, heterochrony, and gives examples of each.

Let us see what is left for recapitulation. Assume for the moment that an ideal ontogeny is composed of a series of stages (a, b, c, d,.....) corresponding to a phylogenetic series of adults (A, B, C, D, ...). To this we may add new terminal stages (i, ii, iii, iv,.....) corresponding to new types of adults arising in evolution (I, II, III, IV,.....). Unless the period of ontogeny is lengthened the series must be reduced by a shortening of the period allotted to each of its stages and eventually to the omission of some, *e.g.*, c, e and h. The series now takes the form: (a, b, d, f, g,.....z, i, ii, iii, iv).

But new characters may also appear by interpolation and without corresponding adult types. These caenogenetic characters may be represented individually (1, 2, 3, 4, etc.). Their appearance will result in further abbreviations and omissions and we arrive at such a series as: (a, 1, d, 2,.....z, i, 8, vi).

Now heterochrony comes upon the scene and our original series by reversal of stages may become thoroughly scrambled in the order: (a, 1, p, 4, 2, d..... 8, z, i, vi). It will now require the services of an embryological cryptographer to decipher the evolutionary meaning in terms of A, B, C, and I, II, III.

Yet in spite of these opportunities for misinterpretation the embryological record is often curiously reminiscent of ancestral history. The pharyngeal region of the vertebrate with its kaleidoscopic mosaic of cartilages, pouches, blood vessels and endocrine glands seems replete with evidences of recapitulation. The larval forms of parasitic animals often afford the only evidence of their systematic relationships. Vestigial structures,

such as the human appendix, seem explicable only on the presumption of embryological conservatism. If the theory of recapitulation is due for retirement, how shall we explain these curiosities of embryology?

LILLIE'S MODIFICATION OF THE RECAPITULATION THEORY

Lillie (1908) attempted a modification of the theory by directing attention to the inheritance of the ontogeny as a whole as a basis for recapitulation rather than the inheritance of the adult condition. In so doing he retains the idea of terminal additions as well as of intermediate modifications. This follows from his premise that "phylogenetic variations are germinal in their character . . . ." and "that every phase of development of every part has two aspects, viz.: the modern, specific, or coenogenetic, and the ancestral or palingenetic aspect."

In a diagram intended to illustrate his theory he represents the stages of an ancestral species thus: A, B, C, D. A second species derived from the first retains all the ancestral stages, but in a modified form, and with added terminal stages (A^1, B^1, C^1, D^1, E). A third species derived from the second retains the stages of species "D" and "E" but even more highly modified (A^2, B^2, C^2, D^2, E^1, F). It will be noticed that in this series the later stage "E^1" has the appearance of having undergone less modification than the earlier "D^2," but this is undoubtedly a fault of the diagram, for the author states explicitly: "In the course of evolution terminal or late stages of the life history are modified more rapidly in a visible morphological sense, and earlier stages are more conservative in the same sense. Hence ancestral resemblances adhere incomparably longer to the embryo than to the adult."

Another deficiency inherent in this graphical representation of the theory is indicated by Professor Lillie in connection with the fact that in the inheritance of ancestral ontogenies the elements of each ancestral stage are so dispersed that no one of these stages hangs together as a unit. Some idea of this corollary may be attempted by breaking up each of the symbols employed for an ontogenetic stage into symbols representing the elements concerned. Thus we might formulate the ontogeny of species "D" and "E" as follows:

Aa	Ba	Ca	Da		Aa^1	Ba^1	Ca^1	Da^1	Ea
Ab	Bb	Cb	Db		Ab^1	Bb^1	Cb^1	Db^1	Eb
Ac	Bc	Cc	Dc		Ac^1	Bc^1	Cc^1	Dc^1	Ec
Ad	Bd	Cd	Dd		Ad^1	Bd^1	Cd^1	Dd^1	Ed
Ae	Be	Ce	De		Ae^1	Be^1	Ce^1	De^1	Ee
Af	Bf	Cf	Df		.	.	.	.	.
Ag	Bg	Cg	Dg		.	.	.	.	.
.	.	.	.		.	.	.	.	.
.	.	.	.		.	.	.	.	.

By the omission of some stages and retardation of others the ontogeny of species "F" would read (in part):

Ba^2	Ca^2	Ca^2	Da^2	Ea^1	Fa
Ab^2	Ab^2	Cb^2	Eb^2	Eb^1	Fb
Ac^2	Bc^2	Cc^2	Dc^2	Ec^1	Fc
.	.	.	.	.	.

A glance at this series indicates that, if the lower-case letters be taken to refer to individual organs or organ-systems, the general course of their evolution may be traced from one embryological stage to another although the stages themselves may have been so broken up as to be unrecognizable. It was with this in mind that I stated (1927) that the theory of recapitulation "is not applicable to the embryo as a whole, but only to individual organs or systems of organs."

De Beer seems to be in general agreement with the position taken by Lillie, although he does not refer to it in text or

bibliography, for he says (page 102), "If only the recapitulationists would abandon the assertion that that which is repeated is the *adult* condition of the ancestor, there would be no reason to disagree with them."

It is an interesting sidelight on the status of the recapitulation theory among embryologists that, while many of them have investigated the organogeny of many different animals and have arrived at certain conclusions concerning the phylogeny of these groups, few have made use of their material to prove or disprove the validity of the theory itself. The most ardent advocates of the Haeckelian theory have been found among the anatomists and paleontologists, who have not the opportunity of observing how the different embryological stages arise one from the other, nor the problem of analyzing the functions of the different elements associated in each stage.

The Haeckelian recapitulationists knew nothing of modern genetics and very little experimental embryology. They were fancy free in dealing with heredity and the physical forces involved in development. Hence they could refer to a mysterious heredity and conclude that an adult might in some occult sense determine the course of development in the offspring, even though the characters transmitted were acquired in the Lamarckian sense. So Weismann, stern critic of the Lamarckian theory that he was, could write (1904): "The ontogeny arises from the phylogeny by a condensation of its stages."

This concept is not accepted so easily in the twentieth century. Lillie insisted that phylogenetic variations must be germinal in nature. From which it follows that the ontogeny is determined not by any changes in the adult structure of the ancestor *per se*, but by modifications in the germplasm of the ancestor which, in all probability, did not produce any effects in its adult appearance.

THE GENE THEORY IN RELATION TO THE RECAPITULATION THEORY

The modern theory of the gene, as developed by Morgan (1926), finds application here. These hypothetical units, located in the chromosomes, are transmitted from parents to offspring and so serve to perpetuate hereditary characteristics. The mechanism by which the genes are transmitted is, in bisexual species at least, such as to allow a considerable latitude of variation within specific limits but to preserve the characteristics of the species from generation to generation. No matter how environmental influences affect the ontogeny of any individual, the genes which the latter deals out to its immediate descendants are derived from, and identical with, those received from its immediate ancestors. No characteristics acquired after the embryonic period can be tacked on to the ontogeny of the offspring except insofar as the latter are also exposed to the same environmental influences. Certainly there is no evidence of any kind which would lead us to believe that new genes producing terminal effects are added to the assortment with which the individual is endowed at the moment of fertilization.

On the contrary new characteristics have been shown to be the result of mutations on the part of the genes themselves and it has been demonstrated by Müller (1928) that such mutations can be induced directly by environmental stimulation, *i.e.*, radiation. It is, of course, possible from a theoretical point of view that genes might be modified by parallel induction in both germinal and somatic cells, in which case, if the effects of the mutant genes were not lethal and happened to be visible, we should witness the

appearance of a new *and* transmissible characteristic such as is postulated by the theory of the inheritance of acquired characteristics. A similar result would occur from a viable and visible mutation in an embryonic (stem) cell destined to produce both germinal and somatic cells. Such an event must be exceedingly rare from the theory of probabilities, and all the evidence at our disposal indicates that most mutations are lethal, that few produce visible effects, and that the most favorable time for the appearance of mutation is during the maturation of the germ cells.

An important, for our purposes, conclusion to be drawn from recent genetic literature is that the effects of a gene mutation are not limited to a single somatic characteristic. Several cases of multiple effects have been analyzed to show that a single mutation affects different parts and functions of the body and at different times in ontogeny. This affords an explanation of heterochrony, for early stages in development may be modified as well as later ones. The activity of mutations is by no means terminal alone.

However, it is obvious that gene mutations affecting early stages in development are apt to produce more serious anomalies than those whose results appear later in ontogeny. They are, therefore, more likely to prove lethal and to disappear. But even so there is no reason to consider that persistent mutations add terminal stages to the ontogeny for, while lengthening of the embryonic period has been observed in mutant fruit-flies, the point at which such lengthening takes place is usually during the larval rather than in later stages.

The limits of effectual modification of an ontogeny as a result of mutant genes are to be found in the essentially epigenetic nature of development. Every stage, or element of a stage, forms a link in a continuous chain of cause and effect. Any mutation which so modifies any part of any stage that a self-maintaining and fertile individual does not develop can not be perpetuated. A mutation which inhibited cleavage, if such a possibility can be imagined, would be fatal to a multicellular species. One which prevented the development of a free-swimming larva, such as the trochophore, would tend to annihilate a sedentary or parasitic aquatic form. So in each large group of animals we should expect to find verification of von Baer's law that the ontogenies resemble each other most closely in early stages and differ in later stages.

The principle of multiple effects on the part of the gene may be invoked to explain the appearance of vestigial, *i.e.*, apparently functionless, structures. For in the aggregation of genes shared by the members of a derived species there may be one which induces the appearance of the primordium of an ancestral organ in addition to other effects. The gene persists by virtue of the other effects and because of its persistence the organ in question must make its appearance although its later development may be retarded or suppressed.

THE ORGANIZATOR THEORY

But it is not well to call an organ functionless prematurely and it has ever been the history of anatomy to discover new functions for so-called vestigial structures —witness the present interest in the endocrine glands. And the recent development of the organizator theory in the hands of Spemann (1928) and others offers a new interpretation for embryonic vestiges. These investigators have demonstrated that certain embryonic structures, *e.g.*, the dorsal lip of the blastopore in vertebrates, serve as organizing centers which induce differentiation in surround-

ing tissue. Such delicate experiments as the transplantation of a bit of presumptive ectoderm into the gastrular cavity of another salamander egg, where it becomes chorda-mesoderm, indicate the function of position in determination. And when such transformed tissue is grafted beneath the ectoderm of another gastrula and induces the appearance of a neural plate above it, it is clear that the grafted tissue organizes the hitherto undifferentiated tissue near it.

It follows that although each embryonic cell may have a complete complement of identical genes, its position with respect to other cells comes to play an increasingly important part in determining its later development. The factors involved in determining the location of the organizators remain obscure, although the existence of the axial gradients demonstrated by Child (1915) may push the problem still further back. At any rate we have reason to believe that the dorsal lip of the blastopore in the amphibian egg exists, not as a reminiscence or recapitulation of the open blastopore of an invertebrate animal, but as an organizator necessary to later development. So many of the so-called vestiges of embryology may prove to play leading rôles in the development of the individual. This idea seems complementary to a famous dictum of Lillie (1895): "In fact the cell is a builder which lays one stone here, another there, each of which is placed with reference to future development."

A consideration of these biological developments, utterly foreign to the biological background of the early Haeckelians, taken with the many observational departures from the embryological sequences demanded by the theory of recapitulation, as well as the logical difficulties arising from an examination of the theory itself, seems to demand that the hypothesis be abandoned. Those of us who were reared in the phylogenetic tradition may see it go with a sigh of regret. Those of us charged with the responsibility of expounding the law of evolution to our classes will miss a familiar maxim, easily learned, and a convenient skeleton on which to hang the discrete data of embryology. But there can be no excuse for continuing to impress plastic minds by means of discredited generalizations. Let us rather return to the laws of von Baer and explain the resemblances which these describe in terms of processes rather than of precedents. The resemblances may indicate close evolutionary relationships. Or they may result from convergent evolution. Only the methods of comparative anatomy, itself deductive, or of palaeontology can indicate which. It is the function of the embryo to become an adult without looking backward on ancestral history. It is the business of the embryologist to describe the phenomena which he observes in terms of individual development without undue attention to what can be interpreted at most as reminiscences of evolution.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE TITANOTHERES OF ANCIENT WYOMING, DAKOTA, AND NEBRASKA. *In two volumes. Department of the Interior, U. S. Geological Survey, Monograph 55.*

By Henry Fairfield Osborn. U. S. Government Printing Office, Washington. $9.00 for set of 2 volumes. 9 x 11½; Vol. I, xxiv + 701 + 42 plates; Vol. II, xi + 251 + 236 plates; 1929.

In the space available it is impossible to do justice to this great monograph, which required some twenty years for its preparation, and nine years more before its publication. So far as we are aware the evolution of no group of animals has ever been so thoroughly and comprehensively studied, described, and brought into relation with what is known about evolution generally as is that of the Titanotheres in these two massive and beautifully produced volumes. This study may fairly be said to mark the highest point that vertebrate paleontology has yet reached. Furthermore, in the highest sense, it is a contribution of major importance to general biology.

The results and conclusions likely to be of greatest interest to the readers of THE QUARTERLY REVIEW OF BIOLOGY, since considerations of space compel a choice, are those concerning the methods of evolution in this group. They are as follows:

The present aspects of the evidence appear to be as follows:

Intervariation selection: There is no evidence that minute individual variations, except immunity to disease, have been a cause of the origin or evolution of new characters.

Interfluctuation selection: There is considerable evidence from both paleontology and zoölogy that the selection of fluctuations of proportion may have been a potent factor in evolution.

Interrectigradation selection: There is no reason to believe that minute rectigradations, in their most rudimentary stages, have sufficient survival value in competition with other biocharacters to affect the life of an organism.

Interorgan selection: It is demonstrated that single structures, organs, or functions can certainly be the causes of survival or extinction, especially under conditions of stress of environment—biologic or physical.

Interindividual selection: The chief action of selection between individuals seems to be to standardize—to keep every individual as a whole up to or above the average of adaptability of the group to which it belongs. Individuals that combine the largest number of favorable, adaptive, and adaptable characters are constantly being selected. In this process organic or coincident selection plays a large part.

Intergroup selection: By a study of local adaptive radiation of the titanotheres we have discovered many separate lines of descent in which similar biocharacters were evolving at different rates. There has been more or less competition between these groups, varieties, races, and species. Here we observe especially the survival of the unspecialized forms and the extinction of the extremely specialized forms.

Intergeneric, subfamily, family, and superfamily selection: The principle just stated applies to selection in relation to the survival or elimination of subfamily, family, and superfamily divisions.

To sum up: Natural selection appears to be operating incessantly and positively to preserve and accumu-

late characters that have survival value and to eliminate all other characters. Numerical reduction within a group and even extinction may be due to a single eliminating cause or to a combination of eliminating causes.

LE PROBLÈME DE L'ÉVOLUTION.

By Maurice Caullery. Payot, Paris. 40 fr. 5½ x 9; 447; 1931 (paper).

The first half of this book is devoted to an exposition of the general character of the arguments which show that evolution has taken place. The second half is devoted to a consideration of the mechanism behind the facts. Professor Caullery comes to the conclusion that none of the theories so far advanced can be considered as satisfactory; Lamarck's theory is contrary to the weight of the evidence; natural selection can act only on mutations; and mutations, so far as observation has gone, do not seem to furnish an adequate basis for the actually observed differences in species. We can merely say, therefore, that evolution has occurred, but why it should have occurred is still a mystery.

The book is well and clearly written. Our most serious criticism is of a certain carelessness in historical matters. Naudin's name is carefully coupled with Mendel's; but neither Erasmus Darwin, Samuel Butler, nor Hering are mentioned in connection with Lamarck and Semon.

PLANT LIFE THROUGH THE AGES. *A Geological and Botanical Retrospect.*

By A. C. Seward. Including Nine Reconstructions of Ancient Landscapes Drawn for the Author by Edward Vulliamy. The Macmillan Co., New York. $10.00. 6 x 9; xxi + 601; 1931.

It is unfortunate that the cost of this book will prohibit it from reaching many interested readers. It has been compiled for the layman and students of botany and geology from the author's four volume text-book on Fossil Plants with the aim to illustrate the nature of the documents from which geologists have compiled a history of the earth, or at least such scraps of history as can be written from the material that is available; to give some account of the methods employed in the interpretation of the documents; and to present in language that is not unnecessarily technical a summary of the more interesting results obtained from records of the rocks which throw light on the development of the plant-world.

The pleasing form in which the volume is issued, its not too formidable contents, as well as the numerous excellent illustrations will appeal to many readers. A lengthy bibliography has been added for those who wish to go to the original sources. There is an index.

UP FROM THE APE.

By Earnest A. Hooton. The Macmillan Co., New York. $5.00. 6¼ x 9¼; xvii + 626; 1931.

In this book Professor Hooton deals with the evolution of the various primates, the development of the individual man from the egg to the grave, fossil remains of man, and contemporary races. We recommend it to the intelligent layman who wishes to learn something about physical anthropology and the evidence of man's evolution. The factors which have brought about evolution are obscure, but the theory which Professor Hooton thinks the least improbable is that in earlier stages environment is the dominating influence, while in higher stages the intelligence of the organism itself directs its evolution by selecting or molding the environment.

GENETICS

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 356.*

Containing following articles: *Arbeitsweise der botanischen Phylogenetik und anderer Gruppierungswissenschaften,* by Walter Zimmermann; *Methoden zur Darstellung versteckter mendelnder Erbanlagen durch ihre Aktivierung ohne Kreuzung,* by Walter Schultz. *Urban und Schwarzenberg, Berlin.* 11 marks. 7 x 10; 172; 1931 (paper).

In this number of the Abderhalden *Handbuch* Professor Zimmermann contrasts the phylogenetic method of classification with

the intuitional, while Doctor Schultz shows how the pigmentation of hair and iris by cold may be used to make hidden Mendelian factors manifest. These are both first-rate pieces of work. The former, especially, should be of interest, not only to taxonomists and geneticists, but to all biologists.

HEREDITY. *Second Edition.*

By A. Franklin Shull. McGraw-Hill Book Co., New York. $3.00. 5½ x 9; xv + 345; 1931.

The first edition of this excellent text was reviewed in Volume I of this journal. In this second edition new phenomena, such as allelomorphism and lethal homozygotes, and new experimental results bearing on evolution have been introduced. The chapter on immigration has been revised to fit the present laws and administrative procedure, and that on the population problem, to accord with the new census and other recent statistical results.

GENERAL BIOLOGY

A SHORT HISTORY OF BIOLOGY. *A General Introduction to the Study of Living Things.*

By Charles Singer. Oxford University Press, London. 18 shillings net. 5½ x 8½; xxxv + 572; 1931.

THE STORY OF LIVING THINGS. *A Short Account of the Evolution of the Biological Sciences.*

By Charles Singer. Harper and Bros., New York. $5.00. 5¾ x 8⅝; xxxv + 572; 1931.

These two volumes are the English and the American editions respectively of easily the most satisfactory history of biology for the use of students yet to appear in any language. With a firmly established reputation as a medical historian the distinguished author has now turned his attention to general biology with most happy results. These books are substantially identical except for the title page. We shall therefore speak of them as one.

This is a treatise on the development of biological ideas, beginning with the Greeks and tracing the gradual decline of all scientific inquiry through the Dark Ages, to be born again with the humanistic and naturalistic movements of the sixteenth century, until with Vesalius and Harvey the foundations of modern biology are laid. In the seventeenth and eighteenth centuries came great developments; first those associated with the introduction of the microscope, then classification, comparative anatomy, geographical distribution, paleontology, all finally culminating in the idea of evolution, with Buffon, Erasmus Darwin, and Lamarck as the great figures. On the developments up to this point Singer uses a little more than half his space. The remainder of the book traces, in separate chapters, the development of the principal special fields of modern biology: cytology, physiology, relativity and integration of functions, biogenesis, embryology, sex, and heredity.

The book is written in a simple, clear and charming style, which holds attention like a novel. We think the judgments and viewpoints to be on the whole as sound as they are stimulating. The book is profusely and usefully illustrated. Altogether it is unusual that we feel moved to recommend a book so unreservedly as we can this to all students of biology, young and old.

RECENT ADVANCES IN MICROSCOPY. *Biological Applications.*

Edited by A. Piney. P. Blakiston's Son and Co., Philadelphia. $3.50. 5¼ x 8; vii + 260; 1931.

This book is mainly made up of a discussion of recent cytological methods and results in the fields of botany, zoology and medicine, with the addition of a chapter on the microscopy of the living eye which is not usually thought of as a part of microscopy. The sections are as follows: I. The medical sciences, by A. Piney; II. Microscopy of the living eye, by Basil Graves; III. Zoology, by E. W. MacBride and H. R. Hewer; and IV. Botany, by E. C. Barton-Wright. The sections on zoology and botany contain extensive reference lists. The illustrations, while

not numerous except in the chapter on the microscopy of the living eye, are well done. There is an index.

A TEXTBOOK OF EXPERIMENTAL CYTOLOGY.

By J. Gray. The Macmillan Co., New York; Cambridge University Press, Cambridge. $7.50; 25 shillings. 6 x 9; x + 516; 1931.

This book presents the substance of a course of lectures given at Cambridge University, where the author is lecturer in experimental zoology. Stress is put upon the fundamental complexity of living matter. The topics treated are: The cell as a unit of life; the cell as a physical unit; cell dynamics; the cell as a colloidal system; the physical state of protoplasm; cell membranes and intercellular matrices; the nucleus; mitosis; cell division; the shape of cells; the growth of cells; cell variability; the equilibrium between a living cell and water; the permeability of the cell surface; the nature of the cell surface; the germ cells; contractile cells; phagocytosis. Each chapter is well documented. The numerous tables, figures and drawings form a valuable part of the book. There are author and subject indexes. An important addition to the substantial textbook literature of biology.

OCEANOGRAPHY. *Its Scope, Problems, and Economic Importance.*

By Henry B. Bigelow. Houghton Mifflin Co., Boston and New York. $2.50. 5 ¼ x 8; vii + 263; 1931.

This book forms part of a survey on oceanography made under the auspices of the Natural Academy of Sciences to consider "the share of the United States of America in a world-wide program of oceanographic research." Professor Bigelow has written a book which will be not only stimulating to the student of these problems but will also be of much interest to the general reader. He discusses the present condition of oceanographic research and some of the outstanding problems under the following headings: Submarine geology; physical and chemical problems of the sea water; relationship between oceanography and meteorology; life in the sea; economic value of oceanographic investigations; and physical, chemical, geologic and biologic unity in the sea. There is no index.

A NATURALIST'S VOYAGE ROUND THE WORLD IN H. M. S. 'BEAGLE.' *The World's Classics, CCCLX.*

By Charles Darwin. Oxford University Press, New York. 80 cents. 3½ x 5⅞; vi + 530; 1930.

It is appropriate that on the centenary of the sailing of the *Beagle* a new edition of Darwin's famous journal should be published. Although one of the most important sections explains his theory of the origin of the atolls of the Pacific and Indian Oceans, the greater part of the book is devoted to South America and the adjacent islands. We find Darwin occupied with the problems of the geographical distribution and extinction of species, which later led him to the concept of the origin of species through natural selection. There is a foreshadowing of the latter in the discussion of checks on the increase in numbers of a species and in the following passage on the finches of the Galapagos Islands:

> Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends.

THE WISSAHICKON HILLS. *Memories of Leisure Hours Out of Doors in an Old Countryside.*

By Cornelius Weygandt. University of Pennsylvania Press, Philadelphia. $4.00. 6 x 9; xiii + 366; 1930.

We find ourselves somewhat embarrassed in attempting to review this book. It should be done by a literary fellow with a gift for saying good things well, and not by one whose style, if any, has been mainly influenced by scientific "literature." But

we have enjoyed the book enormously, and it seems only fair to tell our readers so. The book is

> made out of many memories of boyhood, a good few of youth, and a steadily lessening number from subsequent years, from early manhood, from middle age and from the edge of old age. The most of the chapters were written in my thirties, and practically all of them from the angle of those years. They have some of them been in print before, in magazines. They make up a book almost wholly of out-of-doors, by one who has cared more for walking across country and for noting the little wonders seen by the way than for any other kind of leisure. There is a portion of it observations made doing chores about the place, working in the garden, pottering about.

LES COAPTATIONS CHEZ LES INSECTES. *Supplément XIII au Bulletin Biologique de France et de Belgique.*

By Jean Corset. Laboratoire d'Évolution des Êtres organisés, Paris. 85 francs. 6½ x 10; 337; 1931 (paper).

The term coaptation was borrowed by Cuénot from medical language, to indicate the reciprocal adjustment of independent parts to form an apparatus with a definite function, comparable in the human sphere to a hook and eye, a tongue and groove, or mortise and tenon. They are frequent and well developed in the chitinous members of insects. The present work begins with a morphologic study, with particular emphasis on the Coleoptera; physiological and biological sections follow, and finally a philosophical consideration of the origin and evolution of coaptations, and their bearing on the problem of purpose. The author does not believe that Lamarckian or Darwinian explanations, or mutations, can account for the facts; and he holds that the facts demand an intelligence transcending the insect.

ECONOMIC BIOLOGY FOR STUDENTS OF SOCIAL SCIENCE. *Part II. Animal and Vegetable Products.*

By Philippa C. Esdaile. University of London Press, London. 10 s. 6 d. net. 5⅜ x 8½; xv + 231; 1931.

We have had occasional critics who complained that American universities offer instruction in cookery and interior decorating. With such reactionaries we have no sympathy; and we are accordingly glad to learn that the University of London includes King's College of Household and Social Science, in which Doctor Esdaile is reader in biology. The present work is Part II of her treatise, Part I of which was noticed here in Volume III, Number 1. It would seem well designed for courses in domestic science.

LA CULTURE DES TISSUS EN BIOLOGIE EXPÉRIMENTALE.

By Emile C. Craciun. Masson et Cie, Paris. 55 francs. 6½ x 10; vii + 440; 1931 (paper).

An excellent summary, with especial emphasis on technique, of the work which has been done on tissue cultures. The book is copiously and well illustrated, has a bibliography covering 57 pages of fine print set close, and a detailed index. We commend this book as a most useful review which should be in every biological library.

DER BIOLOGE. *Monatsschrift zur Wahrung der Belange der deutschen Biologen. 1. Jahrgang, Heft 1.*

Edited by O. Appel, E. Baur, Ph. Depdolla, M. Hartmann, A. Kühn, E. Lehmann. J. F. Lehmanns Verlag, Munich. 7 marks one-half year; 6 marks one-half year to members of the Verband Deutscher Biologen; 1.40 marks, single copy. 6½ x 10; 34; 1931 (paper).

The official organ of a recently established professional union of German biologists.

TEXTBOOK OF GENERAL BIOLOGY.

By Waldo Shumway. John Wiley and Sons, New York. $3.00. 5¾ x 9; viii + 361; 1931.

A textbook designed for students not planning to specialize in botany or zoology.

BIOLOGICAL TYPES AND PRINCIPLES. *A Laboratory Manual.*

By Henry R. Barrows. Richard R. Smith, New York. $2.00. 5½ x 8½; xii + 395; 1931.

A laboratory guide for a course in general biology, primarily correlated with the author's text *College Biology*, but capable of being used with any standard text.

CAN SCIENCE EXPLAIN LIFE?

By Carl F. Krafft. Carl F. Krafft, Box 1421, Washington, D. C. $1.00. 4⅞ x 7; 94; 1931.

A revised and enlarged edition of Mr. Krafft's "Spirazines," which was noticed in Vol. VI.

PROBLEMS IN BIOLOGY.

By George W. Hunter. American Book Co., New York. $1.76. 5¼ x 8; xii + 706; 1931.

BIOLOGY NOTEBOOK.

By W. H. D. Meier and Dorothy Meier. Ginn and Co., Boston. 72 cents. 7½ x 10½; viii + 160; 1931 (paper).

HUMAN BIOLOGY

LA FERTILITÁ DEI BIOTIPI. *Saggio di Demografia Costituzionalistica. Pubblicazioni della Università Cattolica del Sacro Cuore. Serie Ottava: Statistica, Vol. IV.*

By Marcello Boldrini. Società Editrice "Vita e Pensiero," Milano. 20 lire. 6½ x 10; xiii + 238; 1931 (paper).

This interesting investigation was undertaken to test the doctrine held rather generally by constitutionalists to the effect that individuals of the broad (pyknic) type are characterized by more intense sexual reaction and activity than individuals of the long (asthenic) type. A group of 715 families in and near Padua was studied, with the critical safeguards on the statistical side of the work to be expected from the distinguished author.

The results were in accord with the theory stated above: the pyknic type parents produced, on the whole, more children than the intermediate type parents, and these in turn more than the asthenic type parents. This was particularly marked in the suburban dwelling and peasant families included, as is indicated by the following figures:

Average number of children of the peasants after elimination of influence of the wife's age at the time of marriage and the length of the fecund conjugal period:

Broad-shaped types	7.96
Middle types	7.55
Long-shaped types	7.01

The differences are significant. In this way, by the statistical experiment the differential fertility is proved and it depends on the different sexual reaction of biotypes.

After obtaining these results the author goes on to discuss other general questions and in the end concludes that a part of the reason, at least, for the lower fertility of the upper classes is to be found in the preponderance of asthenic types among them.

Whether the reader is convinced by the author's data and reasoning or is not, and some will not be because the results and conclusions cut across ingrained prejudices here and there, nevertheless this volume can only be regarded as an interesting and useful contribution to a number of important problems now very much in the forefront of interest.

NEW DISCOVERIES RELATING TO THE ANTIQUITY OF MAN.

By Sir Arthur Keith. W. W. Norton and Co., New York. $5.00. 5½ x 8½; 512; 1931.

With each new discovery concerning man's early forebears the ancient past becomes more alluring. Sir Arthur Keith has produced a book which, although dealing mostly with such subjects as fossil teeth and skull bones, is nevertheless absorbingly interesting from beginning to end. While based more or less on his second edition of

the *Antiquity of Man*, which appeared in 1925, it is really a completely new work including all the important discoveries made within recent years and a discussion of their bearing on the problem of man's march from the distant past. Beginning with the discovery of *Australopithecus* in South Africa, the author leads to a discussion of the relation of the Bushman to the prehistoric inhabitants of South Africa and the antiquity of the Oldoway man and other remains from caves in East Africa. He then proceeds to the Neanderthal types of men and women found in Palestine, and remains taken from old lake beaches in lower Egypt.

Readers will probably find those chapters dealing with the search in China for prehistoric remains, and the great discovery of *Sinanthropus* (the Peking man) the most thrilling in the book. These are followed by a discussion of *Pithecanthropus erectus* from Java and the Cohuna man from Australia. The vast areas of the Americas have produced up to the present time only one type (represented by the Punin skull found in Ecuador) whose recognized antiquity permits it to enter the galaxy of notables already mentioned. Europe furnishes so many examples that most of the latter half of the book is devoted to them. In the final chapter is a discussion of the possibility of *Homo gardarensis*, whose skull was found in a Norse burial ground in Greenland, being a throwback of modern man to the primitive type.

The book is well illustrated with maps, drawings, and charts. There is an index.

ORDER OF BIRTH, PARENT-AGE, AND INTELLIGENCE.

By L. L. Thurstone and Richard L. Jenkins. University of Chicago Press, Chicago. $3.00. 6 x 9; xiii + 135; 1931.

This book is in two parts. The first deals with an analysis of case histories collected at the Institute for Juvenile Research in Chicago. Some of the more interesting findings are:

There appears to be a definite tendency for the intelligence quotient to increase progressively, within sibships, from the first-born to the later birth numbers. This tendency seems to extend past the seventh-born child. While among children of dull, adequate, and superior intelligence it is observed that there is negative correlation between intelligence quotient and size of sibship, there is a low but definitely positive correlation between intelligence and size of sibship within the group of mentally defective children. No clear or definite relation is observed between the individual ages of parents at the time of birth of a child and the intelligence of that child. Parents of nearly the same age have children who appear to test slightly higher in intelligence than those of parents widely different in age. There appears to be some tendency for children born six or more years after their next older sibling to do poorly on intelligence tests.

The second part of the book is devoted to a discussion of the literature on such subjects as the handicap of the first born, fecundity and intelligence, behavior adjustment, effect of parent on weight, mortality and intelligence of the offspring.

There is a bibliography of 167 titles and an index.

THE FIRST TWO YEARS. *A Study of Twenty-Five Babies. Vol. I. Postural and Locomotor Development.*

By Mary M. Shirley. University of Minnesota Press, Minneapolis. $2.00. 5¼ x 7½; xv + 227; 1931.

This book deals with only part of the results of an extensive investigation on the development of 25 infants during a period of two years. Two other volumes will appear later on (1) intellectual development and (2) personality manifestations. Dr. Edith Boyd, who assisted Dr. Shirley in the collection of the data, will report on the physical growth and physiological development of the infants. The present study gives in detail an analysis of the pattern of motor development, individuality in motor development and specific phases. The volume contains eight appendices exhibiting record sheets and data. There are also tables, figures and plates in the text, a bibliography of 40 titles, and an index.

THEORIES OF POPULATION FROM RALEIGH TO ARTHUR YOUNG.

By James Bonar. Greenberg, Publisher, New York. $3.50. 5½ x 8½; 253; 1931.

In this series of Newmarch lectures the author of *Malthus and His Work* deals with pre-Malthusian theories of population. In the political writings of Raleigh, Bacon, Hobbes, and Harrington, there are scattered *obiter dicta* on population, but the first writer who seems to have thought of basing his work on a statistical study of the facts was Graunt. In spite of the defects of the Bills of Mortality he succeeded in establishing the stability of chronic diseases, the excess of male over female births, the high death-rate in infancy, and the excess of urban over rural death-rates. He had also the idea of a life table, but as the Bills of Mortality did not give the age at death, his table was little more than a guess. Halley was able to do better on the basis of material from Breslau. Süssmilch in the course of his application of vital statistics to natural theology developed the former. The account continues through the controversy between Hume and Wallace over the relative populousness of ancient and modern nations, through Price with his fear of the depopulation of England, to Young, the scientific agriculturist.

HANDBOOK OF ETHNOGRAPHY.

By James G. Leyburn. Yale University Press, New Haven. $5.00. 5½ x 8½; ix + 323 + 6 maps; 1931.

The usefulness of this book not only to ethnologists, but to students of anthropology, archaeology and allied sciences, can hardly be overestimated. The author gives the names of over 12,000 tribes, language groups, nations, clans, and other social divisions, their locations, and references to maps at the end of the book where the geographical homes of these peoples can be found. The names of geographical and political divisions of the world are also given (these in small capitals to differentiate them from peoples and tribes). In order to keep the book within serviceable limits it was impossible to include all towns, rivers, mountains, bays, etc. For this reason Sumner and Keller's *The Science of Society* was used as a basis of selection. The location of every geographical spot mentioned in it is given. Under the headings East Indies, Melanesia, Micronesia and Polynesia are listed several hundred Pacific islands. Following the main part of the book is a section giving a *Table of Peoples* arranged under the political divisions of the world. Each of the six maps at the end of the volume covers two pages.

In compiling this book the author makes no claim to completeness. However, it will rarely be found lacking desired information. The volume should be on the reference shelves of all working libraries.

PLARR'S LIVES OF THE FELLOWS OF THE ROYAL COLLEGE OF SURGEONS OF ENGLAND. *Volumes I and II.*

Revised by Sir D'Arcy Power, with the Assistance of W. G. Spencer and G. E. Gask. John Wright and Sons, Bristol. 42 shillings net, cloth; 57 s. 6d. net, half leather. 6½ x 10; Vol. I, xxvi + 752; Vol. II, 596; 1930.

The Order of Fellows of the Royal College of Surgeons of England was founded in 1843. These two volumes here noticed contain in alphabetical order brief biographical accounts of all the deceased Fellows. The spade work for the volumes was done by Victor Gustave Plarr (1863–1929) who was the Librarian of the College from 1897 until his death. His notes were edited and revised for publication by Sir D'Arcy Power, with the assistance of Mr. W. G. Spencer and Prof. G. E. Gask, all Fellows of the College. The result is a contribution to medical history of first-rate importance. It is proposed to issue a supplement every ten years. There is an author index, which seems a labor of supererogation in view of an alphabetical arrangement of the text. An analytical subject index would have cost a good deal of labor, but would have enhanced enormously the value of the work to the student. Suppose, for example, one wishes to study the group of Fellows who specialized in genito-urinary

surgery, or the group who combined writing poetry with the practice of surgery. There is no way, as the book stands, by which the persons who fall in such groups can be found except by reading all the biographies.

HEALTH ON THE FARM AND IN THE VILLAGE. *A Review and Evaluation of the Cattaraugus County Health Demonstration with Special Reference to its Lessons for Other Rural Areas.*

By C. -E. A. Winslow. The Macmillan Co., New York. $1.00. 5½ x 8½; vii + 281; 1931.

This report of one phase of the activities of the Milbank Memorial Fund should be widely circulated, as it furnishes a valuable guide to all those interested in public health activities in rural communities. Dr. Winslow finds the work to have been planned with great wisdom and to have been carried out efficiently and economically. The survey shows that the full-time county health unit is effective and practical and can be supported in an average New York county. With adequate funds it is held that such a unit may be developed to a point in advance of the type of organization often considered as "standard" for rural areas, and that such development is economically justified by direct returns in the saving of human life. The records indicate an annual saving of 34 lives, the greatest being among infants. There was a marked reduction in deaths from tuberculosis as well as a definite reduction in the number of known cases.

THE PHYSICAL CHARACTERS OF THE SOCIETY ISLANDERS. *Based on Field Records by E. S. Craighill Handy and Willowdean C. Handy. Memoirs of the Bernice P. Bishop Museum, Vol. XI, No. 4.*

By H. L. Shapiro. Bernice P. Bishop Museum, Honolulu. $1.25. 9½ x 12¾; 113 + 4 unnumbered; 1931 (paper).

This is part of an extensive study on the racial composition of the Polynesian people. The author presents the data with explanations of methods, notes on population, distribution, variability and inter-island differences. Under the heading "Comparative Notes on the Society Islanders" is discussed the results which an analysis of the anthropometric measurements yield. All available data indicate that the Society Islanders are a heterogeneous group. The distributions of their anthropometric characters reveal a marked tendency towards bi-modal and multi-modal curves. Although the series is not large, the significance of these distributions is enhanced by the occurrence of similar distributions among other Polynesian groups. In fact, the recurrence of identical modes in the curves of the various island groups offers one method in the attempt to disentangle the diverse elements in the Polynesian race. Not only the analysis of these curves but geographical comparisons as well, indicate the existence of several types. Geographical segregation may be observed in head length, head width, and cephalic index. But the uniformity of means and of multi-modal curves found in other traits suggests that the heterogeneity characteristic of the Polynesians may be of old standing and already existing, to some extent, anterior to their invasion of Polynesia.

The measurements upon which the study is based are arranged in 40 tables. Included in the paper are photographic plates of the various types.

THE CASE FOR ACTION. *A Survey of Everyday Life Under Modern Industrial Conditions, with Special Reference to the Question of Health.*

By Innes H. Pearse and G. Scott Williamson. With Prefaces by Lord Moynihan and A. D. Lindsay. Faber and Faber, London. 5 shillings net. 4¾ x 7½; xii + 171; 1931.

Uplifting schemes generally stimulate an avoiding reaction in us. We have examined with more or less care a large number, and find that the proportion which we can approve even mildly runs well below the legal limit of one half of one per cent. We approached the present volume in a very bilious mood, expecting to find another scheme for elevating the incompetent at the expense of the thrifty. For once we seem to have been wrong; a moderately careful examination has not revealed the catch in the proposal. Actually, this is an account of the work done at the Peckham Pioneer Health Centre in the last four years, and a state-

ment of what is proposed for the future. The work seems to avoid a good many of the undesirable features of such projects, and to possess a number of virtues not ordinarily associated with health-improvement schemes. A particular virtue is that the work has been, and is to continue, self-supporting. Each family pays weekly dues (6*d*. a week in the past, to be raised to 1*s*. in the future), and it is calculated that after covering operating expenses there will be a margin of around £1,000 per annum to repay the cost of the building. Even our chronic narrow-mindedness can find little to object to in an uplifting enterprise that pays its own way in this manner.

GENIUS AND CREATIVE INTELLIGENCE.

By Nathaniel D. Mstron Hirsch. Sci-Art Publishers, Cambridge, Mass. $4.50. 6¼ x 9½; 339; 1931.

This book is divided into three parts. In Part I the author traces man's socio-historical development, and concludes that geniuses have been the greatest *single* factor in this development.

Part II is concerned with the psychological constitution of man.

Part III gives an historical and analytic summary of three groups of conclusions concerning genius reached by writers and investigators in the last three quarters of a century, namely: (1) a negative view of genius, in which genius is biologically linked with insanity, imbecility and degeneracy; (2) a positive view of genius, in which genius is considered a quantitative increase of the faculties common to man; and (3) a view which regards genius as qualitatively different from talent. The author tends to hold the last of these views.

THE RACES OF JAVA. *A Few Remarks Towards the Acquisition of Some Preliminary Knowledge Concerning the Influence of Geographic Environment on the Physical Structure of the Javanese.*

By D. J. H. Nyèssen. G. Kolff and Co., Weltevreden, Dutch East Indies. Fl. 4.50. 7 x 10½; viii + 122; 1929.

This is in the nature of a preliminary report, and for this reason the results herein presented are considered by the author not definitely conclusive until an analysis of the large amount of material collected has been completed. It includes a statement of the principles on which the investigation is being carried out, a summary of the plans, a short report of the work and a somatological description of the population of a small mountain district. The complete analysis of the data will yield much of interest not only concerning the influence of geographical environment on the physical structure of the Javanese, but on a wide variety of allied topics. At the present stage of the investigation all indications point to the population of Java being divisible into "three groups, an Eastern, a Western and a Meridional group. The first is probably of South Mongolian, the second of Dravido-Australian origin. Side by side with Asiatic components, the third group possibly embraces elements resembling the Meridionals of Africa." The work includes sketches of types, maps, statistical data on the mountain-dwellers, a literature list, and an index.

ESSAYS ON POPULATION AND OTHER PAPERS. *Together with Material from His Notes and Lectures.*

By James A. Field. Compiled and Edited by Helen F. Hohman. With a Foreword by James Bonar. University of Chicago Press, Chicago. $3.50. 5½ x 8¼; xxix + 440; 1931.

The essays on population in this volume fall into two classes, historical and critical. Among the former are narratives of the Malthusian controversy in England, of the early propaganda for birth-control in the 1820's and its recrudescence in the '70's, and of the eugenic movement. Among the latter one of the most interesting is that in which Professor Field questions whether eugenic worth and economic value run parallel. As his editor notes, he was fonder of putting questions than of

giving the answers. There are also papers on logarithmic diagrams and on the place of economic theory in graduate work, an outline of Field's course on the standard of living, and a bibliography of books and pamphlets on population in his library.

THE CHILD FROM ONE TO SIX. *His Care and Training. United States Department of Labor, Children's Bureau Publication No. 30. Revised January 1931.*

U. S. Government Printing Office, Washington. 10 cents. 5¾ x 9⅛; v + 150; 1931 (paper).

This is a revised edition of the bulletin which was issued in 1918 under the title *Child care—the preschool age*. It has been entirely rewritten and brought up to date. For the small sum of ten cents the interested parents can have at hand all the necessary information concerning the rearing of the young child, as well as much sound advice on habit forming and mental development. This bulletin is written in a simple, direct way so that it may be easily comprehended. Doctors, district nurses and social workers will find it highly useful. The work contains a number of illustrations, a chart on communicable diseases, a book list and an index.

AN HYPOTHESIS OF POPULATION GROWTH.

By Ezra Bowen. Columbia University Press, New York. $3.75. 5¾ x 8¾; 238; 1931.

The immediate factors that determine population growth are birth rates and death rates and, to a lesser extent, migration. What are the factors that in turn determine these immediate factors? Professor Bowen, being an economist, naturally thinks of these in economic terms and takes as his formula: "Population size tends to vary directly with aggregate wealth, and inversely with the height of standards of living." He concludes further that with the probable rise in the standards of living the growth of the various populations will soon halt, that the world is not in danger of starvation through overpopulation, that the 'rising tide of color' will be checked, that poverty will be eliminated and the risk of war reduced, and that with universal birth control the differential birth rate will become eugenic rather than dysgenic.

NOGUCHI.

By Gustav Eckstein. Harper and Bros., New York. $5.00. 6 x 9¼; ix + 419; 1931.

The author makes a bold attempt to give life to this biography of a distinguished bacteriologist by writing it in the style of what he apparently regards as a Japanese thinking in English. After a while one gets used to it, but we are still of the opinion that a better case could have been made for Noguchi by a less artificial method of presentation. In any event the story of a man who had such a colossal store of nervous energy, coupled with extraordinary technical skill, makes interesting reading. But in the end the feeling is that once more it is made evident that it is impossible for Occidentals really to understand Orientals.

THE MAKING OF MAN. *An Outline of Anthropology.*

Edited by V. F. Calverton. The Modern Library, New York. 95 cents. 4 x 6½; xv + 879; 1931.

In this Golden Treasury of anthropology are included selections dealing with various aspects of fossil and prehistoric man, race and language, social organization, sexual customs and social practice, religion, and evolution of attitudes. The different points of view of the main schools of anthropology are represented, as well as selections from writers, such as Bachofen, whose work, although outmoded, is of importance in the history of the subject. In the introduction Mr. Calverton develops his theory of cultural compulsives—the bias towards doctrines which subserve the interest of one's group. No man can escape this bias, but "the awareness of the compulsive nature of

social thought should make it possible for the development of a little more flexibility and a little more criticism within the radius of the *cultural compulsive* itself."

MEDICINE, SCIENCE AND ART. *Studies in Interrelations.*

By Alfred E. Cohn. University of Chicago Press, Chicago. $4.00. 6 x 8⅞; xiii + 212; 1931.

Dr. Cohn states in his preface his reasons for writing the stimulating and penetrating essays in this book:

> By nature, medicine is empirical, as is all natural science, and requires no apology for being so. But to be intellectually respectable it must, as I think, have well-defined functions, clear sanctions for existence, and a conscious direction. Not to have a policy is also a policy, but one which does little credit either to the historical sense or to the intellectual fertility of its responsible leaders. A policy, in short, medicine must have—or perhaps I should say, *I* must have. And so I have made one, as these essays show. Since I began to reflect on these matters, I have become emboldened in continuing this adventure by the fact that, in other disciplines as well, similar urgencies have been experienced. Many volumes published by physicists, beginning in this era with Ernst Mach, and an equal number by biologists, the recent one by Woodger being especially welcome to me, attest to a need like mine in other men in very different walks of inquiry.

PERIODICITY, RHYTHM AND SYMMETRY WITH THE BIRTHS *in 1698 Amsterdam families of six and more children. Statistical Communications of the Municipal Bureau of Statistics of Amsterdam No. 91.*

By G. Wolda. J. M. Meulenhoff, Amsterdam. 2.50 florins. 6½ x 10; xiii + 238; 1931 (paper).

In this interesting paper the author concludes that there is a periodicity in births due in part to seasonal factors and in part to a preponderant birth-rhythm of 19 months and that children conceived at the optimum period have a lower mortality than those conceived at other times. These are difficult statistical questions: it is not entirely clear to us that his conclusions necessarily follow from his data.

NATIVES OF THE WARIA, WILLIAMS AND BIALOLO WATERSHEDS. *Territory of New Guinea, Anthropological Report No. 4,* and (in same volume) NOTES ON THE NATIVES OF SOUTH BOUGAINVILLE AND MORTLOCKS (TAKU). *Territory of New Guinea, Anthropological Report No. 5.*

By E. W. Pearson Chinnery. Commonwealth of Australia, Canberra, Australia and Australia House, London. 16 shillings net. 5⅞ x 9½; 156; no date (paper).

STUDIES OF THE NATIVE POPULATION OF THE EAST COAST OF NEW IRELAND. *Territory of New Guinea, Anthropological Report No. 6.*

By E. W. Pearson Chinnery. Commonwealth of Australia, Canberra, Australia and Australia House, London. 6 shillings net. 5⅞ x 9½; 50 + 3 folding pages; no date (paper).

In this excellent series, previous numbers of which were reviewed in our issue of September, 1931, the Government Anthropologist of the Territory of New Guinea gives data on the physical characters, social organization, demography, etc., of the tribes visited.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 362.*

Containing following articles: *Methoden zur Konservierung von Organen und ganzen Organismen,* by Gustav Schmeidel; *Anthropologische Messungen am lebenden Menschen,* by Richard H. Post. *Urban und Schwarzenberg, Berlin.* 4.80 marks. 7 x 10; 96; 1931 (paper).

In this number of the Abderhalden *Handbuch* Dr. Schmeidel explains the various methods for the preservation of organs and whole organisms and the advantages of paraffin preparations, while Dr. Post describes the different methods of measurement used by nineteen leading anthropologists, and emphasizes the importance of an agreement on standard methods.

KRIMINALPSYCHOPATHOLOGIE UND PSYCHOBIOLOGISCHE VERBRECHERKUNDE. *Zweite wesentlich erweiterte und verbesserte Auflage.*

By Karl Birnbaum. Julius Springer, Ber-

lin. 16.50 marks (paper); 18.80 marks (bound). $6\frac{1}{4}$ x $9\frac{1}{2}$; x + 304; 1931.

A systematic and comprehensive work in which the author approaches his subject of general criminology from the fields of pathology and psychology. This second edition is especially marked by a revised and enlarged treatment of the theory of environment and the psychological and psychobiological theories of crime and punishment.

THE BANTU TRIBES OF SOUTH AFRICA. *Reproductions of Photographic Studies. Vol. II, Section II, Plates XXVII-LII. The Suto-Chuana Tribes. Sub-Group II, the Bapedi (Transvaal Basotho). With an Introductory Article on the Bapedi and Descriptive Notes on the Plates by Werner Eiselen.*

By A. M. Duggan-Cronin. Deighton, Bell and Co., Cambridge, England. 21 shillings. $8\frac{1}{2}$ x $11\frac{1}{2}$; 26 + 26 plates; 1931 (paper).

Section II of Volume II of this valuable anthropological study maintains the high standard of the previous sections which have received notice in earlier numbers of this journal. It contains a short introductory article on the Bapedi, a bibliography, and twenty-six excellent photographic plates with descriptive notes.

THE MOTHERS. *The Matriarchal Theory of Social Origins.*

By Robert Briffault. The Macmillan Co., New York. $4.00. $5\frac{3}{4}$ x $8\frac{1}{2}$; 319; 1931.

A discussion of the central thesis of the author's three-volume work reviewed here in Volume III. The present volume will naturally be found easier reading; our own prejudice, however, is to the effect that the value of the earlier work was at least as much due to its accumulation of material from the literature as to the theories advanced.

ARCHAEOLOGY OF THE ARKANSAS RIVER VALLEY. *Department of Archaeology, Phillips Academy, Andover, Mass.*

By Warren K. Moorehead. With Supplementary Papers on The Prehistoric Culture of Oklahoma, by Joseph B. Thorburn; and The Exploration of Jacobs Cavern, by Charles Peabody. Yale University Press, New Haven. $4.00. 8 x 9; x + 204; 1931.

The Arkansas River rises in Colorado and passes through Kansas, Oklahoma, and Arkansas. It thus traverses culture areas varying from the Cliff-dweller to the Mound-builder types. The present volume contains considerable valuable material which may assist in the solution of problems of origin and dispersal of prehistoric cultures in the region.

THE GREAT PHYSICIAN. *A Short Life of Sir William Osler.*

By Edith Gittings Reid. Oxford University Press, New York. $3.50. 6 x $8\frac{3}{4}$; ix + 299; 1931.

This short biography, by an intimate Baltimore friend of the Oslers, will fill a useful purpose as a supplement to Harvey Cushing's classic. It is pleasantly written and effectively illustrated. The aim is to make clear the extraordinary charm and vitality of the man Osler. His was an elusive spirit, but Mrs. Reid has succeeded well in capturing something of it and transferring it to her pages.

WOMEN IN INDUSTRY. *A Series of Papers to Aid Study Groups. Bulletin of the Women's Bureau, No. 91.*

By Mary E. Pidgeon. U. S. Government Printing Office, Washington. 15 cents (paper). $5\frac{5}{8}$ x $9\frac{1}{8}$; viii + 79; 1931 (paper).

THE RUINS AT KIATUTHLANNA, EASTERN ARIZONA. *Smithsonian Institution, Bureau of American Ethnology, Bulletin 100.*

By Frank H. H. Roberts, Jr. U. S. Government Printing Office, Washington. 65 cents. $5\frac{3}{4}$ x 9; viii + 195; 1931.

METHODS AND STATUS OF SCIENTIFIC RESEARCH. *With Particular Application to the Social Sciences.*

By Walter E. Spahr and Rinehart J. Swenson. Harper and Brothers, New York. $4.00. 5½ x 9½; xxi + 533; 1931.

An undistinguished book on the technique of research, particularly in the historical and social fields. There is little to which violent exception can be taken, and it may be that the book will serve a useful purpose as a textbook in one of the "formal courses in methodology," the lack of which the authors deplore.

GRØNLAND, *dets Natur, Beboere og Historie* (Greenland, Its Nature, Inhabitants, and History).

By Th. N. Krabbe (with an English translation by Annie I. Fausbøll). Levin and Munksgaard, Copenhagen. Dan. Cr. 30 (paper); Dan. Cr. 36 (cloth); Dan. Cr. 42 (½ leather). 9½ x 12¼; xvi + 129 + 170 plates + 8 pages index; 1929 (paper).

An interesting account of the geography, population, and history of Greenland, elaborately illustrated with photographs by the author. A useful as well as attractive volume.

THE RAPE OF TEMPERANCE.

By James A. Reed. Farrar and Rinehart, successors to Cosmopolitan, New York $2.00. 5 x 7⅞; vii + 307; 1931.

Anti-prohibition propaganda.

JUVENILE-COURT STATISTICS, 1929, *Based on Information Supplied by 96 Courts. Third Annual Report. United States Department of Labor, Children's Bureau Publication No. 207.*

U. S. Government Printing Office, Washington. 15 cents. 6 x 9; ii + 61; 1931 (paper).

ZOÖLOGY

A STUDY OF THE TEIID LIZARDS OF THE GENUS CNEMIDOPHORUS WITH SPECIAL REFERENCE TO THEIR PHYLOGENETIC RELATIONSHIPS. *Smithsonian Institution, United States National Museum Bulletin 154.*

By Charles E. Burt. U. S. Government Printing Office, Washington. 80 cents. 6 x 9¾; viii + 286; 1931 (paper).

One of the most widespread groups of lizards in the Western Hemisphere is the genus *Cnemidophorus*. Up to the present time much confusion has existed concerning the number of forms, their relationship, distribution, and differentiation, one from another. This is due to many factors. The extremely varying habitat (the range is from southern Brazil to northern United States) and the apparently natural tendency for the forms to vary, the intricate series of pattern stages which many species show during development, the abnormalities which frequently occur in various populations, together with the fact that the genus itself has never been clearly defined and that some of its oldest species have been wrongly placed, have all served to make the study of this group extremely difficult. It was to bring order out of chaos that the present work was undertaken. Something over 12,000 specimens from widely scattered localities have been examined in establishing relationships of the now known forms. No new species have been found. Many forms have been linked as subspecies. Certain differences in the genus, such as melanism, or the type of mesoptychial scutellalion, were found to be largely environmental in nature.

The records and discussions are given in great detail. For each species there are sections on general and systematic notes, diagnosis, description, variation, range, habitat, general behavior, life history, enemies and affinities. The work includes a key, diagrams of relationships, figures, distribution maps, a lengthy bibliography, and an index.

HYDROSTATICS OF THE SUCTORIAL MOUTH OF THE LAMPREY. *University of California Publications in Zoölogy, Vol. 37, No. 2.*

By T. Emmett Reynolds. University of California Press, Berkeley. 30 cents. 7 x 10¾; 20; 1931 (paper).

The author of this study on the mechanics of the head and tongue of the lamprey gives the following summary of his work:

> Studies made on living lampreys by means of the x-ray show a striking example of adaptation of body structure to fit the peculiar life-habits of these animals. By means of artificial feeding the movements of the various parts involved were controlled to permit of careful observation and their function determined during actual operation.
>
> A hydro-sinus was discovered to be part of the hydrostatic equipment, serving as a storage chamber whence water could be forcibly ejected by contraction of the pharyngeus anterior muscle, in this manner cleansing the branchial tract of foreign substances. It is believed likewise that this hydro-sinus maintains the vacuum in the post-lingual region by ejecting leakage water and food past the velar valve.
>
> A mechanical description of the feeding-pumping cycle is given. This description is based on the above observations as well as by inference from studies on the gross anatomy of the tongue and oral region.

A MONOGRAPH OF THE EXISTING CRINOIDS. *Volume I. The Comatulids. Part 3. Superfamily Comasterida. Smithsonian Institution, U. S. National Museum Bulletin 82.*

By Austin H. Clark. U. S. Government Printing Office, Washington. $2.00. $9\frac{3}{4}$ x $12\frac{1}{4}$; 853 + 81 plates; 1931 (paper).

A careful, thorough piece of taxonomic research, beautifully illustrated with halftone plates, and dealing with the single family Comasteridae. The difficulties presented by the comatulids, as well as an interesting thought for the geneticists, are indicated in the following statement (p. 66):

> The comatulids are exceptionally difficult animals to identify. Many of them are very variable, so variable that different individuals may present a widely different aspect. This is especially true in those species in which the number of arms varies between wide extremes, in which the number of elements in the division series is subject to much variation, and in which the arms vary very greatly in relative length. It is particularly true in the comasterids.
>
> It not infrequently happens that two comasterids with the same number of arms belonging to species of different genera will resemble each other more closely than either resembles others of its own species with a different number of arms.

THE BIRDS OF HAITI AND THE DOMINICAN REPUBLIC. *Smithsonian Institution, United States National Museum Bulletin 155.*

By Alexander Wetmore and Bradshaw H. Swales. U. S. Government Printing Office, Washington. $1.00. 6 x $9\frac{3}{4}$; iv + 483; 1931 (paper).

Hispaniola, the name given by Columbus to the island now occupied by the Republic of Haiti and the Dominican Republic, is biologically the most interesting of the West Indies group. In the mountainous regions have been found many interesting forms which are remnants of types which have become extinct elsewhere in the West Indies. The Smithsonian Institution is in possession of an extensive and valuable collection of animals and plants from this and adjacent islands and reports on the different animal groups are in the process of preparation.

The account on birds has been written by Doctor Wetmore, although much preliminary work was done by Mr. Swales before his death in 1928. The first part of the volume is devoted to an historical account of biological expeditions. This the reader will find extremely interesting. The total list of birds reported, excluding 13 doubtful ones, is 215. Of this number the larger part is found in the coastal or interior plains or lower hills. A much smaller group is confined to the high mountains of the interior and it is in this group that are found the rare specimens. A brief section is devoted to lists of birds found on some of the small nearby islands. The volume contains a lengthy bibliography and an excellent index.

INSECTS AND CLIMATE. *Transactions of the Entomological Society of London, Vol. 79, Part I.*

By B. P. Uvarov. With a prefatory note by Capt. A. F. Hemming. Entomological Society of London, London. 11 shillings. 7 x $10\frac{3}{4}$; 247; 1931 (paper).

A valuable survey of the literature. The first part deals with the experimental physiology of insects, the second with the influence of the climatic environment in nature. The author believes that climatic factors largely control the numbers of insects in nature, and is disposed to minimize the importance of parasites and predators.

He also distrusts, one gathers, mathematical and theoretical investigations. Whether one agrees with him on these points or not, his work will be found of great value. His bibliography includes about 1150 titles.

INVERTEBRATE ZOÖLOGY. *Second Edition.*

By Harley J. Van Cleave. McGraw-Hill Book Co., New York. $3.00. 5¾ x 9; xiv + 282; 1931.

This second edition contains a considerable number of changes. Aside from a general rewriting of most of the chapters and the addition of new illustrations, the sections on the Protozoa and Porifera have been radically changed to bring the contents up to date. Much material of general biological interest has been added throughout the book and less emphasis has been placed on morphology and taxonomy. Specific sections on the orders have been omitted for most of the chapters, while the outlines of classification have been placed at the close of the discussion of each phylum. All of these changes have increased materially the usefulness of the book either as a text for strictly morphological courses or for general courses in invertebrate zoölogy. The book is well documented and indexed.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung XX.*

Edited by G. Grimpe and E. Wagler. Akademische Verlagsgesellschaft, Leipzig. 6.80 marks. 6 x 8½; 84; 1931 (paper).

Earlier numbers of this valuable work have been noticed in these columns. This part contains the following articles: Introduction to the geology of the North and Baltic Seas, by Otto Pratje; Parasitic flagellates, by Eduard Reichenow; and Spirochetes, by Margarete Zuelzer.

BAR-RAC. *The Biography of a Raccoon.*

By Vance J. Hoyt. *Lothrop, Lee and Shepard Co., Boston.* $1.50. 5¼ x 8½; 111; 1931.

Bar-Rac, a raccoon cub, was brought up from infancy in the household of Dr. Hoyt, for scientific purposes. Her experiences, and those of her companion and fellow-mischief-maker, a gray fox cub, as related in this book should interest both children and grown-ups.

REPORT ON A GAME SURVEY OF THE NORTH CENTRAL STATES. *Made by Aldo Leopold for the Sporting Arms and Ammunition Manufacturers' Institute under Direction of its Committee on Restoration and Protection of Game.*

American Game Association, Investment Bldg., 15th and K Sts., N.W., Washington. $1.00. 6¾ x 9¾; 299; 1931.

An account of the status of wild game in Michigan, Ohio, Indiana, Illinois, Minnesota, Wisconsin, Iowa, and Missouri. The investigation was financed by the sporting arms industry, for obvious motives. The report contains much interesting information, and many suggestions of unsolved problems, in connection with natural population equilibria.

BIRD LIFE AT THE POLE.

By Wolcott Gibbs. W. Morrow and Co., New York. $2.00. 5 x 7½; 171; 1931.

A mildly humorous attempt at satirizing the Byrd Expedition to the South Pole.

THE BLUE BOOK OF BIRDS OF AMERICA. *A Bird Guide Containing the Following Orders of Birds: Goatsuckers, Swifts, etc.; Perching Birds, including theTyrant Flycatchers, Larks, Crows and Jays, Starlings, Icteridae, and Finches.*

THE GREEN BOOK OF BIRDS OF AMERICA. *A Bird Guide Containing the Orders of Perching Birds including Tanagers, Swallows, Waxwings, Shrikes, Vireos, Warblers, Pipits, Dippers, Mimic Thrushes, Wrens, Nuthatches, and Creepers, Titmice, Wren Tits, Kinglets, Gnatcatchers, and Thrushes.*

THE RED BOOK OF BIRDS OF AMERICA. *A Bird Guide Containing Diving Birds, Swim-*

mers, Herons, Storks, Ibises, Marsh Dwellers, Shore Birds, Pigeons and Doves, Birds of Prey, Cuckoos and Woodpeckers.

By Frank G. Ashbrook. Whitman Publishing Co., Racine, Wis. 10 cents single copy; Set of 3 in box, 50 cents. $3\frac{1}{4}$ x $5\frac{1}{8}$; 96 pages each; 1931 (paper).

Useful popular field guides.

A New Pocket Gopher from Southeastern California. *University of California Publications in Zoölogy, Volume 38, No. 1.*

By Joseph Grinnell. University of California Press, Berkeley. 25 cents. $7\frac{1}{8}$ x $10\frac{3}{4}$; 11; 1931 (paper).

Studies on the Oyster Drill (*Urosalpinx cinerea, Say*). *United States Bureau of Fisheries Bulletin No. 4.*

By Henry Federighi. U. S. Government Printing Office, Washington. 20 cents. $7\frac{1}{2}$ x 11; 33; 1931 (paper).

Juvenile and Sex Characters of Evorthodus Lyricus (*Fam. Gobiidæ*). *United States Bureau of Fisheries Bulletin No. 5.*

By Isaac Ginsburg. U. S. Government Printing Office, Washington. 5 cents $7\frac{3}{8}$ x 11; 8; 1931 (paper).

Goldfish: Their Care in Small Aquaria and Ponds. *United States Bureau of Fisheries, Fishery Circular No. 6.*

By E. C. Fearnow. U. S. Government Printing Office, Washington. 5 cents. $5\frac{3}{4}$ x 9; 16; 1931 (paper).

The Arachnid Order Chelonethida. *Stanford University Publications, Biological Sciences, Vol. VII, No. 1.*

By Joseph C. Chamberlin. Stanford University Press, Stanford University, Calif. $2.00 (paper); $2.50 (cloth). $6\frac{7}{8}$ x 10; 284; 1931.

Handbook of Common Commercial and Game Fishes of California. *Division of Fish and Game of California, Bureau of Commercial Fisheries, Fish Bulletin No. 28.*

By Lionel A. Walford. California State Fisheries Laboratory, Terminal Island. Free. $5\frac{7}{8}$ x 9; 183; 1931 (paper).

BOTANY

Researches on Fungi. *Volume IV. Further Observations on the Coprini together with Some Investigations on Social Organisation and Sex in the Hymenomycetes.*

By A. H. Reginald Buller. Longmans, Green and Co., New York. $8.40. 6 x $9\frac{1}{2}$; xiii + 329; 1931.

In this volume Professor Buller completes his description of the sub-types of the Agaricineae, analyzes the factors concerned in the mechanical fixation of the fruit-body of *Coprinus sterquilinus* in its substratum, deals with social organization in the higher fungi and the physiological advantages which the mycelia derive from their cooperation, by means of hyphal fusions, in the production of a fruit-body, and shows that in *Coprinus lagopus* a diploid mycelium is able to diploidize an appropriate haploid mycelium. The work is an excellent contribution to our knowledge of the fungi.

A Contribution to the Paleobotany of the Eocene of Texas. *Bulletin of the Agricultural and Mechanical College of Texas, Fourth Series, Vol. 2, No. 5.*

By O. M. Ball. Agricultural and Mechanical College of Texas, College Station. $8\frac{3}{4}$ x $11\frac{3}{4}$; 173 + 48 plates + 6 unnumbered; 1931.

The author aims to present as complete as possible a record of the fossil plants known to occur in the Eocene formations of Texas. He gives an outline of the general geologic

features of the region, a non-technical discussion of the origin of sedimentary formations and of fossils in general, and a description of the fossil forms now in the collection of the Agricultural and Mechanical College of Texas and of others which have been reported from the region. There is a short bibliography and an index.

STUDIES ON THE GENUS PYTHIUM.

By Velma D. Matthews. University of North Carolina Press, Chapel Hill. $3.00. 6¾ x 9¾; v + 136; 1931.

In this systematic study of the genus *Pythium*, the author describes all species of the genus and reports on the species which have been isolated by himself. Twenty species of *Pythium*, of which five are new, were studied. Several of these species are reported from the United States for the first time. The first part of the book is taken up with a discussion of methods and culture media, taxonomy, distribution and habitat, cytology, etc. Keys are given for the genera of the family Pythiaceae and the species of the genus *Pythium*. The book is well documented and illustrated. There is an index.

A MITOSE NAS RAIZES DO NOTHOSCORDUM FRAGRANS (VENT. KUNTH).

By S. de Toledo Piza, Junior, and A. Paravicini Torres. Piracicaba, Saõ Paulo, Brazil. 6½ x 9½; 9 + 2 plates; 1931 (paper).

INVESTIGATIONS ON THE SPIKE-DISEASE OF SANDAL. *I. Résumé of Observations Made to Date. II. Report of Progress Made During the Quarter Ending 30th June 1931.*

By N. C. Chatterjee, C. Dover, H. A. H. G. Hicks, J. E. M. Mitchell, M. Sreenivasaya, A. V. Varadaraja Iyengar. Edited by V. Subrahmanyan. Indian Institute of Science, Bangalore. 7½ x 9¾; 16; 1931 (paper).

ENVIRONMENT AND PLANT DEVELOPMENT, *Being "Klima und Boden in ihrer Wirkung auf das Pflanzenleben."*

By Henrik Lundegårdh. Translated and Edited from the Second German Edition by Eric Ashby. Longmans, Green and Co., New York. $9.50. 5¾ x 9; xii + 330; 1931.

The original German edition of this book was reviewed in Volume I of this journal. The present translation is from the second German edition, but does not differ importantly from the original. The work is a useful addition to ecological literature, particularly valuable in its emphasis on the experimental investigation of ecological factors.

A TEXTBOOK OF BOTANY. *For Colleges and Universities. Vol. III. Ecology.*

By John M. Coulter, Charles R. Barnes, and Henry C. Cowles. Revised and enlarged by George D. Fuller. American Book Co., New York. $2.80. 5½ x 8¼; x + 499; 1931.

A FIELD KEY TO THE GENERA OF THE WILD AND CULTIVATED HARDY TREES OF THE NORTHEASTERN UNITED STATES AND CANADA.

By Mary F. Barrett. 64 Park Ave., Bloomfield, N. J. 35 cents per copy; $3.30 for ten copies; $32.00 for one hundred copies. 6 x 9; 40; 1931 (paper).

MORPHOLOGY

FOUR LECTURES ON "THE AETIOLOGY OF IRREGULARITY AND MALOCCLUSION OF THE TEETH."

By J. C. Brash. With an Appendix, "Concerning Orthodontic Problems and Their Solution," by Miss M. L. Tildesley. The Dental Board of the United Kingdom, London. 5 shillings net. 6 x 9½; xi + 274; 1931.

The work deals with the development and growth of the jaws and the factors which

determine their formation. The author, an anatomist, maintains a conservative attitude about the various hypotheses of occlusion that have been suggested in the past.

The problem is considered from the following points of view: (1) The incidence of the phenomena and the probable deductions to be drawn with special reference to the age of onset. (2) 'Nature' as represented by inheritance with its evolutionary background. (3) 'Nurture' as represented by the environmental conditions and control of youth.

This book deserves attention from the orthodontist since it points out that his mechanical technique based upon empiricism and belief in the mechanical cause of malocclusions is not by any means the whole story. There are many factors of inheritance, environment, growth of the facial skeleton, nutrition and others involved, all of which should be taken into consideration when dealing with the causes and nature of malocclusions. An appendix by M. L. Tildesley is devoted to biometric methods and their application to orthodontic problems. The book is well written, profusely illustrated, and ought to prove stimulating to anatomists and orthodontists.

EVOLUTION OF FACIAL MUSCULATURE AND FACIAL EXPRESSION.

By Ernst Huber. The Johns Hopkins Press, Baltimore. $2.50. $6\frac{3}{4}$ x $9\frac{3}{4}$; xii + 184; 1931.

A contribution to a specialized branch of anatomy, which points out the bearing it may have on other branches of biology. The book is primarily devoted to the superficial musculature of the primates, with special emphasis on racial differences in human stocks. While of a highly technical nature, it will probably reward the reader adequately for his trouble. The book would have been easier reading if the plates had been more completely labeled.

AN INTRODUCTION TO NEUROLOGY. *Fifth Edition, Thoroughly Revised.*

By C. Judson Herrick. W. B. Saunders Co., Philadelphia. $3.00 net. 5 x $7\frac{3}{4}$; 417; 1931.

A new edition of an excellent textbook. It should be useful to a wide range of students.

THE DISSECTION OF THE RAT. *Stanford Laboratory Guides, Biological Series.*

By Edwin C. Starks and Richard D. Cutter. Stanford University Press, Stanford University, Calif. 75 cents postpaid. 6 x $8\frac{3}{4}$; 45; 1931 (paper).

MAMMALIAN ANATOMY *with Special Reference to the Cat.*

By Alvin Davison. Fifth Edition, Revised by Frank A. Stromsten. P. Blakiston's Son and Co., Philadelphia. $2.50 net. $5\frac{1}{2}$ x $8\frac{3}{8}$; xiv + 311; 1931.

PHYSIOLOGY AND PATHOLOGY

PHYSIOPATHOLOGIE DE LA THYROIDE: *Diagnostic et Traitement des Goitres.*

By Lucien Dautrebande. Masson et Cie, Paris. 40 francs. 6 x $9\frac{1}{4}$; 326; 1931 (paper).

Dautrebande has written an excellent monograph on the physiological pathology of the thyroid gland. He follows Plummer in stressing the importance of separating the two types of hyperthyroidism: (1) that found in true Basedow's disease (exophthalmic goiter), which develops relatively rapidly without any previous enlargement of the thyroid gland; and (2) the hyperthyroidism which gradually develops in persons with endemic goiter. He admits the difficulty in making the differential diagnosis in individual cases; especially in those in whom exophthalmic goiter suddenly develops in a patient who for years has had a large thyroid. Naturally, the problem is met with most frequently in those regions in which goiter is endemic and commonly seen.

He agrees with Plummer also in regard to the value of giving iodine in Basedow's disease (exophthalmic goiter). Probably because there is little endemic goiter in Belgium he tends to underestimate the danger of giving iodine in large doses to persons who have thyroid tumors. When in Europe in 1926 the reviewer was particularly impressed with the lack of fear shown by physicians in Belgium and Hamburg as they gave iodine to patients about to be operated on for exophthalmic goiter. On the other hand, in Berne and Munich, where endemic goiter is common, the danger of giving iodine was constantly being emphasized. It is this difference in the effects of iodine on patients with certain types of endemic goiter and on those with true exophthalmic goiter that has caused much of the confusion now evident in the literature in regard to the value of the drug and the dangers attached to its use. Much seems to depend on the material which the writer sees: if he lives in a goiterous district he has one opinion, and if he lives where endemic goiter is rare he has another.

The use of iodine as a prophylactic against endemic goiter must, of course, be discussed quite apart from its use in exophthalmic goiter. There are two separate problems here, as Dautrebande clearly shows.

TYPHOID FEVER. *Its Nature, Mode of Spreading, and Prevention.*

By William Budd. American Public Health Assoc., New York. $5.00; De luxe edition, $10.00. 7 x 10; xv + 184; 1931.

A reprint of the classic work in which Budd demonstrated the contagious nature of typhoid fever. In his work as a country practitioner he had had opportunity to observe that, however rife might be the putrescent effluvia which, according to the then accepted pythogenic theory, were the cause of this disease, no epidemic occurred until the introduction of a case of the fever from outside. As means of transmission he emphasized contaminated water, milk, hands and bed-clothing, but he was still enough under the influence of the old theory of miasma to believe that one of the principal ways of communication was by infecting the air.

CHILDHOOD TYPE OF TUBERCULOSIS. *Diagnostic Aids.*

By Eugene L. Opie, Joseph D. Aronson, F. Maurice McPhedran and Henry D. Chadwick. National Tuberculosis Association, New York. 20 cents. 6 x 9; 32; 1931 (paper).

The second edition of a brochure which appeared in 1929 is an excellent and concise guide to clinicians and teachers of clinical medicine. Strong emphasis is given to the fact that there often exists grave tuberculous infection among children who appear perfectly healthy. An interesting and suggestive preface is contributed by Dr. E. L. Opie.

The following subjects are dealt with: Childhood Type of Pulmonary Tuberculosis, by H. D. Chadwick; Introduction to Roentgenographs, by F. M. McPhedran; The Tuberculin Test: Intracutaneous Method, by J. D. Aronson; The Tuberculin Test: Cutaneous Method, by H. D. Chadwick; and Classification of Tuberculous Pulmonary Lesions in Childhood and Adolescence, by F. M. McPhedran.

ANFANGE DES ALTERNS. *Ein psychologischer Versuch.*

By Erich Stern. Georg Thieme, Leipzig. 2 marks. 5½ x 8¾; 46; 1931 (paper).

A study of the melancholy thirties, when one finds his first gray hair and feels the younger generation treading on his heels.

TRAVAUX DU LABORATOIRE DE MICROBIOLOGIE DE LA FACULTÉ DE PHARMACIE DE NANCY. *Fascicule IV.*

By Ph. Lasseur and P. Vernier. Laboratoire de Microbiologie de la Faculté de Pharmacie, Nancy. 6½ x 10; 221; 1931 (paper).

TUBERCULOSIS IN DENMARK, NORWAY AND SWEDEN. *League of Nations, Health Organization. Series of League of Nations Publications III. Health. 1931. III. 1.*

By J. Ostenfeld, N. Heitmann and G. Neander. World Peace Foundation, 40 Mt. Vernon St., Boston; League of Nations, Geneva. $1.50; 6 shillings. 7¼ x 9½; 170; 1931 (paper).

PRINCIPLES AND PRACTICE OF HYGIENE. *A Textbook for College Students.*

By John R. Cain. P. Blakiston's Son and Co., Philadelphia. $1.75 net. 5¾ x 8¾; xiv + 251; 1931.

RECHERCHES SUR LES SPIROCHÉTIDÉS DANS LE DISTRICT DE MONTRÉAL.

By Gérard Gardner. Éditions Médicales, Paris. (Free to individuals or laboratories interested in same work, by applying to G. Gardner, Laboratoire de Biologie, Université de Montréal). 6½ x 10; 88; 1930 (paper).

DELIVERANCE FROM CANCER. *A Vindication of Food Reform and Nature Cure.*

By H. Reinheimer. With Introductory Notes by Charles F. Bennett, Peter Freeman, Harold Mather and Jas. C. Thomson. Rider and Co., London. 5 shillings net. 4¾ x 7¼; 192; 1931.

BIOCHEMISTRY

THE DEVELOPMENT OF PHYSIOLOGICAL CHEMISTRY IN THE UNITED STATES.

By Russell H. Chittenden. Chemical Catalog Co., New York. $4.50. 6 x 9; 427; 1930.

In 1874 the first definitive laboratory of physiological chemistry in the United States was organized in the Sheffield Scientific School at Yale University with Professor Chittenden in charge. The laboratory was a single room accommodating eight students. Since those early days the development of research in this field has been rapid and widespread in America and a survey of this progress covering a period of fifty years is timely. No attempt has been made by the author to give a critical analysis of the work done. Rather has he sought to record what has been accomplished experimentally by investigators either singly or in groups in various parts of the country. Because of the necessity of limiting the size of this volume the material was selected "not alone on the basis of scientific excellence, physiological value, or relative merit, but also with a view to the recognition of the numerous centers of learning throughout the country, both large and small, where physiological chemistry had gained a foothold."

Even with "this very incomplete view" the reader cannot but be impressed with what has been accomplished in the past and the indications for future progress. Such names as Chittenden, Newell Martin, Welch, Bowditch, Mitchell, Porter, Howell and others stand out as pioneers in the field. The foundation of the American Physiological Society in 1887, the *Journal of Experimental Medicine* in 1896, and the *American Journal of Physiology* in 1898, gave added impetus to the development of research work in this field. Today, numerous universities, agricultural experiment stations, hospitals, research institutions, and various government bureaus at Washington have well-equipped laboratories for investigations in physiological chemistry. The *Journal of Biological Chemistry*, established in 1905, contains 84 large volumes filled with contributions by Americans and this represents only one outlet for the publication of research work.

The volume does not include a bibliography, but there is an authors' index and throughout the text are references to papers.

THE VITAMINS.

By H. C. Sherman and S. L. Smith. The Chemical Catalog Co., New York. $6.00. 6 x 9; 575; 1931.

The first edition of this standard text book was concerned with a survey of the knowledge of vitamins to about the end of the year 1921. In the second edition, which brings both the text and the bibliography down to about the middle of the year 1930, "an attempt has been made to summarize the very considerable amount of information which has been gained regarding the chemical natures of the individual vitamins, and the more voluminous knowledge regarding their rôles in life processes, their formation and distribution in nature, their relative abundance in different types of food materials and stability under the conditions to which they are likely to be subjected." Included in the volume are about 180 pages of references, and author and subject indices.

AN INTRODUCTION TO BIOCHEMISTRY.

By Roger J. Williams. D. Van Nostrand Co., New York. $4.00. 5½ x 8½; xiv + 501; 1931.

The author states in the preface, "Specialization has become so narrow that one may take a doctorate degree in organic chemistry and yet be ignorant of the most rudimentary facts relating to the chemistry of organisms." This textbook endeavors to give the student of chemistry some conception of the nature of living processes, so that he may realize that life does not manifest itself always in a series of carbon compounds.

The outline followed by the author, in brief, involves a study of: (1) Composition of the organisms; (2) Food material required by the organisms; (3) Transportation of these food materials into the materials composing the organisms. Section three is the most extensively developed portion of the book, and deals chiefly with the chemistry of metabolism.

The book is clearly and concisely written. It is well suited not only for the student of elementary biochemistry but also for those working in other fields who need at least an introduction into the chemistry of living organisms. In order to use the book to advantage elementary courses in chemistry and biology are necessary. Laboratory experiments are suggested.

A HISTORY OF CHEMISTRY.

By F. J. Moore. Revision Prepared by William T. Hall. McGraw-Hill Book Co., New York. $3.00. 5½ x 8; xxiii + 324; 1931.

This book has an almost epic structure: its theme is the evolution of the fundamental ideas of chemistry and especially of the atomic and valence theories. The great chemists are viewed, not as isolated personalities, but as the champions of the various theories out of which modern chemistry has developed. To us this mode of presenting the history of a science seems admirable.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 354. Dehalogenieren.*

By Hugo Bauer. Urban und Schwarzenberg, Berlin. 5.50 marks. 7 x 10; 107; 1931 (paper).

Technical description of reactions by which the halogens are separated from their aliphatic compounds, leaving unsaturated compounds.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 355.*

Containing following articles: *Die Mikroveraschung als histochemische Hilfsmethode*, by A. Policard and H. Okkels; *Nachweis und Bestimmung der Thymonukleinsäure*, by Zacharias Dische; *Dichroitische Färbung tierischer und pflanzlicher Gewebe*, by W. J. Schmidt.

Urban und Schwarzenberg, Berlin. 6.50 marks. 7 x 10; 109; 1931 (paper).

In this number of the Abderhalden *Handbuch* are given methods for the preparation and examination of ashed sections of tissues, color reactions for thymonucleic acid, and methods of dichroic staining, which supplement the information on the

fine structure of tissues obtained from the ordinary examination by polarized light.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 363. Abt. IV, Angewandte chemische und physikalische Methoden, Teil 1, Heft 6. Fermentforschung.*

Containing following articles: *Methodik des Studiums autolytischer Prozesse*, by L. Utkin and O. Steppuhn; *Manometrische Messung der Eiweissspaltung*, by Hans Adolf Krebs; *Amylase*, by Theodor Sabalitschka; *Tyrosinase*, by Hugo Haehn; *Tannase*, by Ernst Schwab; *Die Bestimmung von Arginin unter Verwendung von Arginase*, by Andrew Hunter. *Urban und Schwarzenberg, Berlin.* 14 marks. 7 x 10; 254; 1931 (paper).

These methods for the study of enzymes are generally of interest to the biochemist. The general biologist may find it worth while to examine the article on autolytic processes.

DIE ROHSTOFFE DES PFLANZENREICHS. *Vierte Auflage. I. Band, Alkaloide bis Hefen. II. Band, Hölzer bis Zucker.*

By Julius von Wiesner. In collaboration with F. Boas, K. Bournot, W. Figdor, E. Gilg, R. Hofmann, O. Kallmann, E. Konstanty, W. Krüger, H. Melchior, J. Messner, F. Schneider, P. N. Schürhoff, J. Weese, H. Wolff, S. Zeisel, A. Zimmermann. Edited by Paul Krais and Wilhelm von Brehmer. Wilhelm Engelmann, Leipzig. 46 marks per volume (paper); 49 marks per volume (cloth); 52 marks per volume (half-leather). $6\frac{1}{8}$ x $9\frac{1}{4}$; vii + 2253; 1927–1928.

The fourth, thoroughly revised, edition of a standard work of reference, indispensable to botanists and technological chemists.

SPECTROGRAPHIC ANALYSIS OF MARINE PRODUCTS. *United States Bureau of Fisheries Investigational Report No. 5.*

By John M. Newell and E. V. McCollum. U. S. Government Printing Office, Washington. 5 cents. $5\frac{3}{4}$ x 9; 9; 1931 (paper).

BIOCHEMICAL AND ALLIED RESEARCH IN INDIA IN 1930.

Society of Biological Chemists, Bangalore, India. $5\frac{1}{2}$ x $8\frac{1}{2}$; 20; 1931 (paper).

SEX

STUDIEN ZUR FERTILITÄT.

By G. L. Moench. Ferdinand Enke, Stuttgart. 12 marks. $6\frac{1}{2}$ x 10; vii + 144; 1931 (paper).

A thorough and penetrating piece of research on diminished fertility and sterility in women. It is a contribution to the physiology of human reproduction of first rate importance.

Among other interesting conclusions reached may be mentioned the following: *Coitus interruptus* as a means of contraception apparently has a harmful effect upon spermatogenesis. Real sexual incompatibility must be rare, because few cases were found in which sterility could not be otherwise explained. Extensive measurements of sperm heads gave no support whatever to the existence of dimorphism, which has been alleged by other workers, particularly in this country. Moench's work is beyond question the most important which has yet appeared upon the biometry and morphology of the spermatozoa of man.

MARRIED LOVE. *A New Contribution to the Solution of Sex Difficulties.*

By Marie C. Stopes. Eugenics Publishing Co., New York. $2.00. 5 x $7\frac{1}{2}$; xiv + 170; 1931.

This volume has been reviewed by Judge John M. Woolsey as follows:

The book "Married Love" does not, in my opinion, fall within these definitions of the words "obscene" or "immoral" in any respect. . . . "Married Love" is a considered attempt to explain to married

people how their mutual sex life may be made happier. . . . The book before me here has as its whole thesis the strengthening of the centripetal forces in marriage, and instead of being inhospitably received, it should, I think, be welcomed within our borders.

THE REMAKING OF MARRIAGE. *A Contribution to the Psychology of Sex Relationship. By Poul Bjerre. Translation by T. H. Winslow. The Macmillan Co., New York.* $2.00. 5⅛ x 7½; viii + 257; 1931.

We are unable to find anything of surpassing value in this book. The author is given to literary expression; and we suspect that he is more interested in striking phrases than in accuracy.

IMPROVED GUIDE FOR THE FITTING AND USE OF HOLLAND-RANTOS DIAPHRAGMS. *Holland-Rantos Co., New York.* Free, to physicians. 6 x 9¼; 23; 1931 (paper).

More directions about how to interfere with the birth-rate, issued by a firm which supplies the utensils.

BIOMETRY

SCIENTIFIC INFERENCE. *By Harold Jeffreys. The Macmillan Co., New York.* $3.25. 5½ x 8½; vii + 247; 1931.

This is a remarkable book in several respects. It contains so far as we know, the first attempt at a mathematical demonstration of Occam's razor—at least, that seems to be essentially what is meant by the statement "the order of decreasing simplicity among laws is also the order of decreasing prior probability."

Whether the demonstration is valid is another question. We have not been completely convinced, as we suspect circularity of argument. Jeffreys' demonstration rests essentially on his theory of probability, which in turn rests on certain postulates. Now Jeffreys' position differs from that of Keynes in that the latter asserts that not all probabilities can be compared in respect of greater or less; this, says Jeffreys, is "one of those attempts at generality that in practice lead only to vagueness." Very good, but is not the argument, then, substantially that Keynes's postulate is less simple than a postulate to the effect that all probabilities are numerically comparable? And, having made this postulate for reasons of simplicity, is it logically sound to use the postulate to prove that simplicity is a fundamental principle? We ask the question because we are in some doubt as to the answer.

The development of probability theory given by Jeffreys is one which rouses a good deal of sympathy in us. It is worth pointing out, perhaps, that his postulates need reworking. He begins with the postulate that all probabilities are comparable in respect of greater and less; in other words, a relation of order always exists between any pair of probabilities. Jeffreys then states that, this being so, we can set up a correspondence between real numbers and probabilities, such that the relation of order among the probabilities is the same as that among the numbers attached to them. But this is not necessarily true, as a simple example will show. Consider a class of number-pairs (x, y), subject to the relation:

$$(x_1y_1) < (x_2y_2) \quad \text{if } x_1 < x_2;$$
$$(x_1y_1) < (x_2y_2) \quad \text{if } x_1 = x_2,\ y_1 < y_2.$$

It is clear that we have thus established a relation of order for all pairs of real numbers; but it is not true that we can set up a correspondence between these number-pairs and the real numbers which will preserve the relation of order which we have established.

The book contains much more than we have so far indicated, and our opinion of it is much higher than perhaps would be inferred from our criticisms. Whether one agrees or not, Jeffreys has much to say which is well worth listening to on probability as well as on sampling, errors of measurement, Newtonian dynamics, and relativity. Our chief regret is the comparative absence of bibliographical reference.

THE MATHEMATICAL PART OF ELEMENTARY STATISTICS. *A Textbook for College Students.*

By Burton H. Camp. D. C. Heath and Co., Boston. $3.60. 5¼ x 7¾; xxi + 409; 1931.

This textbook is intended for an introductory course in statistics to be offered in a department of mathematics to students who have already a knowledge of analytic geometry. It is divided into two parts, which may be given as separate courses. The first is intended to provide a sufficient mathematical introduction to most of the applied courses, while the second deals with probability, sampling, and multiple correlation, besides a more thorough treatment of other topics touched on in the first part. A number of Professor Camp's own results, more accurate approximations than the usual formulae, are given in the chapters on approximations to the point binomial and on sampling.

PSYCHOLOGY AND BEHAVIOR

EXPERIMENTAL PSYCHOLOGY.

By Johannes Lindworsky. Translated from the German by Harry R. DeSilva. The Macmillan Co., New York. $3.75. 5½ x 8½; xix + 406; 1931.

The author of this book, which is in its fourth edition, is head of the psychological department of the German University at Prague, and a member of the Society of Jesus. The translator is associate professor of psychology in the University of Kansas. In the section on morals Professor Lindworsky holds that "the most fundamental *basis of morality* is the absolute will to preserve the most real value, and the *source of knowledge* of the moral commandments is, therefore, none other than the nature created by God." It seems odd that in a treatise on experimental psychology Dr. J. B. Watson's name is not mentioned. Nor do we find Christine Ladd Franklin's name occurring in the section on color vision, the author mentioning only Helmholtz, Hering, and G. E. Müller.

THOUGHT-TRANSFERENCE (OR WHAT?) IN BIRDS.

By Edmund Selous. Constable and Co., London. 7s. 6d. net. 4 x 6¾; xi + 255; 1931.

The author holds that bird behavior is explicable only on the basis of thought transference. The phenomenon which leads him to this conclusion is the simultaneous action—rising, wheeling, and alighting—of flocks of birds. His evidence consists in repeated observation, doubtless as accurate as such observation can be. It seems unlikely that many hard-boiled materialists will be convinced, but Mr. Selous is a good recorder and an entertaining writer, and his book is pleasant reading.

COSMIC CONSCIOUSNESS. *A Study in the Evolution of the Human Mind.*

By Richard M. Bucke. E. P. Dutton and Co., New York. $5.00. 7 x 9¼; xviii + 384; 1931.

Cosmic consciousness, according to the author, is the third and highest type of consciousness. The other two are simple consciousness, which is possessed by the animals, and self consciousness, which is possessed by man. The human race, he holds, is at present developing cosmic consciousness. He instances as those who have had it, Gautama the Buddha, Jesus, Paul, Plotinus, Mohammed, Dante, Bartolomé Las Casas, John Yepes, Francis Bacon, Jacob Behmen, William Blake, Honoré de Balzac, Walt Whitman, and Edward Carpenter, who was peculiar in other ways. We found his account of Bacon more interesting than the others. He holds:

a. That Francis Bacon wrote the "Shakespeare" plays and poems.

b. That he entered into Cosmic consciousness at about the age of thirty, or perhaps a year earlier, as his intellectual and moral development was very precocious.

c. That he began writing the "Sonnets" immediately after his illumination. The "Sonnets," as considered here, are the first one hundred and twenty-six, which distinctly constitute a poem in and by themselves, and deal with the subject here considered.

d. That the earlier of these one hundred and twenty-six "Sonnets" are addressed to the Cosmic Sense, and the later to it and its offspring, the plays.

c. That in the "Sonnets" the following individualities may be recognized: (*a*) the Cosmic Sense; (*b*) the Bacon of the Cosmic Sense, and of the plays and "Sonnets;" (*c*) the special offspring of the Cosmic Sense—the plays; (*d*) the ostensible Bacon of the court, politics, prose writings, business, etc., and possibly others.

MEDICAL PSYCHOLOGY. *The Mental Factor in Disease.*

By William A. White. Nervous and Mental Disease Publishing Co., New York and Washington. $3.00. 6 x 9; v + 141; 1931.

This is not a textbook of psychiatry but a presentation for the medical student of the "principles which are at the basis of an understanding of the psychological factor which is necessarily present in all disease." Dr. White's psychology is wholeheartedly biological. Psychology is the study of the total, as opposed to the partial, reactions of the organism. The psyche has a history of development and evolution as long as that of the body.

The fact that there is a psychological factor in connection with all disease seems to be inevitable if the theory of what constitutes psychological reaction developed in this book is accepted. The specificity of the reaction, however, is the particular thing that now calls for explanation and elucidation. That there is such a specific correlation seems inevitable, but to define it undoubtedly presents one of the most difficult problems of medicine.

JUDGING EMOTIONS FROM FACIAL EXPRESSIONS. *Psychological Monographs, Vol. XLI, No. 3. Whole No. 186.*

By Leo Kanner. Psychological Review Co., Princeton, N. J., and Albany, N. Y. $1.50. $6\frac{3}{4}$ x $9\frac{3}{4}$; iv + 91; 1931 (paper).

Feleky's series of photographs, expressing different emotions, were shown to classes of medical students, who were asked to write down the name of the emotion which they thought was expressed in each picture and the situation which might have given rise to it. The subjects were found to vary widely in ability to judge emotional expression, an ability which was only slightly correlated with intelligence as measured by the Thorndike test.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

A QUARTER CENTURY OF LEARNING 1904–1929 *as Recorded in Lectures Delivered at Columbia University on the Occasion of the One Hundred and Seventy-fifth Anniversary of its Founding.*

Columbia University Press, New York. $3.50. $5\frac{7}{8}$ x $8\frac{3}{4}$; vi + 380; 1931.

Lectures by professors at Columbia, summarizing the advances of the twenty-five years 1904–1929. The various chapters are of somewhat unequal merit; our own vote goes to Professor Wilson, but perhaps that is narrow-minded professionalism. The chapters and their authors are: Introduction (D. R. Fox); History (C. J. H. Hayes); Economics (W. C. Mitchell); Sociology (R. M. MacIver); Government (H. L. McBain); Jurisprudence (Y. B. Smith); Psychology (R. S. Woodworth); Education (W. F. Russell); College administration (H. E. Hawkes); Letters (A. H. Thorndike); Classical studies (F. G. Moore); Architecture (W. A. Boring); Biology (E. B. Wilson); Medicine (W. Darrach); Chemistry (H. C. Sherman); Physics (G. B. Pegram); Engineering (W. B. Parsons); Geology (C. P. Berkey).

STUDENTS' GUIDE TO EFFICIENT STUDY. *A Manual Based on the Results of Scientific Investigation into the Study Habits of College Students.*

By Luella C. Pressey and Jessie M. Ferguson. Richard R. Smith, New York. 35 cents. 5 x $7\frac{3}{8}$; 39; 1931 (paper).